Bark beetles –
between pest species and ecosystem engineers

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Borkenkäfer sind Agenten im Auftrag des grünen Empire,
mit der Lizenz zum Töten.

Jan Baginski 2003: Das silberne Fischbesteck.

Inhalt

Liste der Artikel

Die Thesen dieser Arbeit sind eine Zusammenfassung der Artikel I – VI:

(Artikel I) Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P. 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. Biodiversity and Conservation 17, 2979-3001.

(Artikel II) Müller, J., Noss, R.F., Bussler, H., Brandl, R. 2010. Learning from a „benign neglect strategy“ in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation 143, 2559-2569.

(Artikel III) Bussler, H., Bouget, C., Brustel, H., Brändle, M., Riedinger, V., Brandl, R., Müller, J. 2011. Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. Forest Ecology and Management 262, 1887-1894.

(Artikel IV) Bussler, H., Müller, J. 2004. Borkenkäferzönosen in wärmegetönten Eichenmischwäldern Nordbayerns – Bark beetle communities in oak-mixed-forests on warm stands in Northern Bavaria. Forst und Holz 59, 175-178.

(**Artikel V**) Bussler, H. 2006. Neue Borkenkäferarten in Bayern – Eine Gefahr für Laub- und Nadelbäume – New bark beetle species in Bavaria – danger to deciduous and coniferous trees. Jahrbuch der Baumpflege 2006, 107-112.

(Artikel VI) Bußler, H., Schmidt, O. 2008. Remarks on the taxonomy, distribution and ecology of *Trypodendron laeve* Eggers, 1939 (Coleoptera: Scolytidae). Nachrichtenblatt bayerischer Entomologen 57, 62-65.

1 Einleitung

1.1 Systematik, Biologie und Ökologie von Borkenkäfern

Mit einem Alter von circa 130 Millionen Jahren stammt der älteste paläontologische Nachweis eines Borkenkäfers aus einem Einschluss im libanesischen Bernstein der Unteren Kreide (Kirejtshuk et al., 2009). Die systematische Stellung der Borkenkäfer ist nach wie vor ungeklärt. In der deutschsprachigen Standardliteratur über Borkenkäfer (Postner, 1974; Grüne, 1979; Schedl, 1981; Pfeffer, 1994, 1995), aber auch in neueren internationalen Publikationen (Knizek & Beaver, 2007) werden sie noch als eigenständige Familie *Scolytidae* geführt. Auf Grund verschiedener phylogenetischer und genetischer Studien in der supraspezifischen Taxonomie betrachten sie andere Autoren aber seit längerem nur noch als Unterfamilie *Scolytinae* der Familie *Curculionidae* (Crowson, 1981; Lawrence & Newton, 1995; Hunt et al., 2007). Ein einheitlicher taxonomischer und nomenklatorischer Stand der Borkenkäfer existiert zur Zeit nicht. Alleine bei den mitteleuropäische Arten stehen 119 validen Arten nicht weniger als 180 Synonyma und ungültige Bezeichnungen gegenüber (Schedl, 1981).

Mit weltweit über 5.800 beschriebenen Spezies stellen die Borkenkäfer nur eine bescheidene Anzahl unter den circa 400.000 Arten der Ordnung Coleoptera (Hammond, 1992; Chapman, 2009). Den größten Formenreichtum erreichen sie in den subtropischen und tropischen Regionen. In der Paläarktis sind um 900 Arten bekannt, in Nordamerika über 600 Arten. In Europa liegt die Artenzahl, je nach Definition des Areals, zwischen 250-311 Arten (Pfeffer, 1995; Knizek & Beaver, 2007). Für Deutschland können 109 Arten als zweifelsfrei belegt gelten, darunter vier Adventivarten. Zwar gelten die Borkenkäfer vor allem wegen ihrer wirtschaftlichen Bedeutung als gut untersuchte Gruppe (Pfeffer, 1995; Knizek & Beaver, 2007), jedoch konnten in den letzten Jahren in verschiedenen Regionen Deutschlands etliche Arten in Biodiversitätsprojekten nachgewiesen werden, die beim Monitoring des Forstschutzes bisher nicht erfasst, bestimmt oder ignoriert wurden (Gebhardt, 2003; Bussler, 2006a, c, b; Bussler & Schmidt, 2008). Seit 2002 wird in Nordbayern die Adventivart *Cyclorhipidion bodoanus* (Rtt.), syn. *Xyleborus peregrinus* Eggers, als verbreitete und dominante Borkenkäferart im Kronenstratum von Eichenmischwäldern nachgewiesen (Bussler & Müller, 2004; Bussler, 2006c), auch in Baden und Frankreich ist die Art auffällig häufig, ohne dass sie bisher in neueren Forstschutzpublikationen Beachtung findet.

Die meisten Borkenkäferarten sind in ihrer Entwicklung an Holzgewächse gebunden, nur wenige an krautige Pflanzen oder Samen. Die xylobionten Arten entwickeln sich oftmals räumlich getrennt in Wurzelholz, starkem Stammholz, schwachem Stammholz oder in Ästen und Zweigen. Dass für diese Stratifikation auch interspezifische Konkurrenz verantwortlich

sein kann, zeigen die Interaktion zwischen dem Artenpaar Buchdrucker (*Ips typographus* L.) und Kupferstecher (*Pityogenes chalcographus* L.) mit einer hohen Überlappung der Nischenbreite (Økland et al., 2009) bei den jüngsten Gradationen in Süddeutschland. Der Kupferstecher, der als klassischer Besiedler von schwachdimensioniertem Nadelholz gilt (Escherich, 1923; Postner, 1974; Schwenke, 1974; Schedl, 1981), befiel in Folge des Trockenjahres 2003 stärkste Fichten bis in den Erdstammbereich. Grund dafür war, dass sich die Buchdruckerpopulationen erst aufbauen mussten und somit keine Konkurrenz um Brutraum gegeben war.

Da zwei sehr unterschiedliche Grundtypen der Ernährung bei den xylobionten Spezies vorliegen, werden Arten, die in Bast, Rinde und Splint brüten, als Phloeophage („Rindenbrüter“) und Arten, die im Splintholz Schlauchpilze (*Ascomyceten*) züchten, als Xylomycetophage („Holzbrüter oder Ambrosiakäfer“) bezeichnet (Nüßlin, 1922; Escherich, 1923; Schedl, 1981), wobei sich die Larven der xylomycetophagen Arten ausschließlich mycetophag ernähren (Postner, 1974). Diese Aufteilung ist jedoch fließend, auch bei „echten Rindenbrütern“ konnten Ambrosiapilze (*Ambrosiella* spp.) in verschiedenen Typen von Mycetangien oder auch ohne diese speziellen Organe nachgewiesen werden. In der europäischen Fauna sind zwei Rindenbrüter bekannt, die eine phloemmycetophage Larvalernährung haben. Die ersten Larvenstadien von *Ips acuminatus* (Eichh.) und *Tomicus minor* (Hartig) sind Phloemfresser, die späteren Stadien ernähren sich von den Konidien und dem Myzel von Ambrosiapilzen (Kirisits, 2004). Inzwischen ist davon auszugehen, dass alle Arten, nicht nur die Ambrosiakäfer, in irgend einer Weise mit Pilzen assoziiert sind (Knizek & Beaver, 2007). Von der Symbiose mit Schlauchpilzen profitieren die Käfer dadurch, dass die Pilze Zellinhaltsstoffe des Holzes (u.a. Zucker, Stärke) aufschließen und als Nahrung verfügbar machen. Da Bläuepilzbefall die Wasseradsorption des Splintholzes erhöht (Schmidt, 1994), ist zu vermuten, dass dadurch den Larven auch ein konstanteres Feuchtemilieu der Brutsysteme im abgestorbenen Holz gewährleistet werden kann. Dies dürfte vor allem für xylomycetophage Arten von Vorteil sein. Die direkte Ausbreitungsfähigkeit von Pilzsporen durch Windverfrachtung übertrifft in der Regel die Zoochorie der Sporen durch Insekten um ein Vielfaches. Die Ascosporen der Schlauchpilze sind jedoch in ein schleimiges Substrat eingebettet und somit auf einen Vektor angewiesen. Nicht nur Borkenkäfer, sondern auch andere xylobionte Arten, beispielsweise Bockkäfer (Fam. *Cerambycidae*), transportieren die eingebetteten Ascosporen auf ihrem Ektoskelett beim Dispersionsflug zu neuen potenziellen Wirtsbäumen (Jacobs & Kirisits, 2003). Nach erfolgreichem Einbohren gelangen die Sporen dann direkt in das primäre Keimsubstrat zwischen Bast und Splint. In einer Wechselbeziehung profitieren hiervon wiederum die Holzbesiedler, da die Schlauchpilze frisch infizierte Bäume in ihrer Vitalität schwächen können (Pfeffer, 1995; Kirisits, 2004).

In der Holarktis überwiegt die Phloeophagie, in den Tropen aber die Xylomycetophagie (Beaver, 1979; Schedl, 1981; Pfeffer, 1995). Als Ursache dieser unterschiedlichen trophischen Strategien gelten die große Heterogenität der Gehölzpflanzen der tropischen Waldgesellschaften gegenüber den relativ artenarmen temperaten und borealen Wäldern der Nordhemisphäre, die wesentlich höhere Zersetzungsgeschwindigkeit des Holzsubstrats und die interspezifische Konkurrenz durch andere xylobionte Familien (z.B. Bockkäfer) in tropischen Klimaten, die eine phloeophage Entwicklung für Borkenkäfer erschwert (Beaver, 1979). Die Tropen bieten für eine mycetophage Ernährung auch günstigere Bedingungen, da durch das Fehlen von nichtproduktiven Jahreszeiten Pilzwachstum unter dem warmfeuchten Klima ganzjährig und optimal möglich ist. Hinsichtlich ihrer Wirtspflanzenspezifität unterscheiden sich phloeophage und xylomycetophage Arten deutlich. Rindenbrüter sind meist an eine oder weitere phylogenetisch verwandte Baumgattungen gebunden. Eine absolute Ausnahme unter den Rindenbrütern hinsichtlich seines Wirtsbaumspektrums in Europa ist *Polygraphus grandiclava* Thoms. Die Entwicklung erfolgt sowohl in *Pinus*- und *Picea*-Arten, als auch in *Prunus*-Arten. Die Vermutung, dass es sich um zwei getrennte Arten handelt, konnte bei genetischen Untersuchungen von Populationen aus den Wirtsbaumgattungen nicht bestätigt werden (Avtzis et al., 2008).

Holzbrüter oder Ambrosiakäfer sind in der Regel ausgesprochen polyphag (Postner, 1974; Schwenke, 1974; Atkinson & Equihua-Martinez, 1986; Sauvard, 2007). Ein Beispiel für extreme Polyphagie ist hierbei der Asiatische oder Schwarze Nutzholzborkenkäfer (*Xyleborus germanus* Blandf.), der auch nach Europa eingeschleppt wurde und sich hier etabliert hat (Bussler, 2006c). In Japan wurden 156 verschiedene Gehölzarten als Brutpflanzen der Art dokumentiert (Nobuchi, 1981). Die Wirtspflanzenbeziehungen der Borkenkäfer gelten als gut erforscht (Postner, 1974; Schwenke, 1974; Sauvard, 2007). Zu beachten ist jedoch, dass Imaginalnachweise an Wirtspflanzen nicht zwangsläufig eine erfolgreiche Larvalentwicklung bedingen. Andererseits finden zwischen Pflanzen und phytophagen Organismen permanent koevolutive Prozesse statt, so dass Übergänge auf neue Wirtsarten jederzeit möglich sind, besonders wenn es sich um nacheiszeitlich spät eingewanderte Arten, wie beispielsweise die Rot-Buche (Walentowski et al., 2010) oder um Neophyten handelt (Blaschke et al., 2008; Bertheau et al., 2009).

Das Klima hat in vielfältiger Weise Einfluss auf Borkenkäfer. Horizontale und vertikale Verbreitung, Schwärmzeitpunkt, Dauer der Larvalentwicklung, die Anzahl der Generationen und die Reproduktionsrate werden über die Temperatur gesteuert. Die Aktivitäten unterliegen hierbei Temperaturober- und –untergrenzen (Chararas, 1962). Durch den Klimawandel mit milden Wintern, längerer Vegetationszeit und vermehrten Hitze- und Trockenphasen wird in den temperaten und borealen Regionen der Nordhemisphäre eine Arealerweiterung von Arten und eine Zunahme von Gradationen erwartet (Ungerer et al.,

1999; Logan et al., 2003; Jönsson et al., 2007; Cudmore et al., 2010). Als Indiz für eine vertikale Arealverschiebung unter veränderten Klimabedingungen in den letzten Jahrzehnten steht der Asiatische Nutzholzborkenkäfer *Xyleborus germanus*. Nach Bruge (1995) wurde *Xyleborus germanus* in Europa noch niemals über 500 m nachgewiesen. Nach Henin & Versteirt (2004) war die Art in Belgien nicht in der Lage dauerhafte Populationen über 350 m zu begründen. Inzwischen konnte die Art in Bayern und Baden-Württemberg in Bereichen bis über 600 m reproduzierend nachgewiesen werden. Einzelfunde erfolgten in Höhen bis über 800 m, wobei eine erfolgreiche Larvalentwicklung in diesen Lagen noch zu überprüfen ist (Bussler et al., 2010).

1.2 Borkenkäfer als Forstschädlinge

In Waldökosystemen sind Borkenkäfer entweder ständige Mitglieder der Zoozönose vitaler Bäume oder aber vorübergehend Mitglieder der Teilzönosen kränkelnder oder absterbender Bäume (Pfeffer, 1995). Alle in Europa heimischen Arten werden als Sekundärbesiedler betrachtet, was nicht ausschließt, dass einzelne Arten, speziell der Buchdrucker (*Ips typographus*), nach abiotischen Vorschädigungen, wie Sturmwurf, Schneebruch oder Trockenphasen, bei nachfolgender Gradation „primär“ werden können und gesunde Bäume angreifen und töten (Escherich, 1923; Dingler, 1927; Postner, 1974). Weltweit betrachtet sind Borkenkäferschäden jedoch nur in der holarktischen Nadelwaldzone von Bedeutung, wobei die Gradation des „Mountain Pine Beetle“ (*Dendroctonus ponderosae* Hopkins) in Kanada seit 1994 mit einer Befallsfläche von über 11,3 Millionen Hektar und einem Holzanfall von 240 Millionen m^3 alles bisher Bekannte übertrifft (FAO, 2010). Der Schadholzanfall durch Borkenkäfer in Europa betrug im Zeitraum 1950 bis 2000 durchschnittlich 2,9 Millionen m^3 pro Jahr (Schelhaas et al., 2003), das entspricht 0,7 Prozent der europäischen Holzeinschlagsmenge. Eine Analyse der Schadholzmengen in Europa von 1990 bis 2001 verursacht durch *Ips typographus* L., *Pityogenes chalcographus* L., *Ips acuminatus* (Gyll.) und *Tomicus piniperda* (L.) (Grégoire & Evans, 2004) ergibt mit 1,2 Prozent, bezogen auf den Holzeinschlag, einen ähnlichen prozentualen Wert. An erster Stelle steht hierbei wiederum der Buchdrucker mit einer Schadholzmenge von durchschnittlich 2,64 Millionen m^3 pro Jahr. Zwei Faktoren sind hierfür ursächlich: Massenvermehrungen phytophager Insekten sind in Fichtenwäldern als ein Teil des kontinuierlichen Entwicklungszyklus aufzufassen (Schmidt-Vogt, 1989), außerdem befinden sich in Europa 6 bis 7 Millionen Hektar reine Fichtenbestände außerhalb ihres natürlichen Verbreitungsgebietes (Leitgeb & Gärtner, 2005). Bayern und Baden-Württemberg, die deutschen Bundesländer mit den größten künstlichen Fichtenanbauflächen (www.bundeswaldinventur.de), sind deshalb auch traditionell am stärksten von Buchdruckerschäden betroffen.

Die Hoffnung, mittels Populationslockstoffen große Teile von Borkenkäferpopulationen in diversen Fallensystemen abzuschöpfen bzw. sie von der schutzbedürftigen Vegetation fernzuhalten (Vité, 1978), erfüllte sich nicht. Die hierfür nötigen Fallenmengen waren unter ökonomischen Gesichtspunkten für den Praxiseinsatz nicht rentabel, vor allem kam es durch die Aggregationspheromone zu Stehendbefall im Umfeld der Fallensysteme. Erheblich beeinträchtigt wurden durch die Pheromonfallen auch diverse Nichtzielorganismen, darunter auch räuberische und parasitische Gegenspieler der Borkenkäfer, da die Pheromone auf sie als Kairomone wirken (Hellrigl & Schwenke, 1985; Bußler, 1986).

1.3 Borkenkäfer als Ökosystemingenieure

In der Forstschutzliteratur werden Borkenkäfer unter wirtschaftlichen Gesichtspunkten entweder als schädlich oder als indifferent betrachtet (Escherich, 1923; Dingler, 1927; Schwenke, 1981). Die mit Borkenkäfern vergesellschafteten Organismen wurden zunächst ebenfalls unter Forstschutzaspekten betrachtet, von Interesse waren hierbei hauptsächlich ihre „natürlichen Feinde“ (Escherich, 1923; Dahlsten & Stephen, 1974). Postner (1974) erkannte, dass ihnen unter normalen Populationsdichten, zumindest bei der Aufschließung des Bestandsabfalls, eine gewisse ökologische Bedeutung zukommt. Auf Grund ihrer Funktion für die Lückendynamik und bei der Waldsukzession nach großflächigeren Störungen wurden einige Arten von Amman (1977) und Schowalter et al. (1981) erstmals als „Keystone species“ bezeichnet. Weslien (1992) konnte einen Arthropodenkomplex von über 140 Arten nachweisen, der mit *Ips typographus* assoziiert ist. Ihre Funktion bei der Habitatgestaltung, für die Biodiversität und ihre Rolle als erste Stufe bei der Verjüngung zu naturnäheren Wäldern findet inzwischen zunehmend Beachtung (Dahlsten & Stephen, 1974; Weslien, 1992; Martikainen et al., 1999; Byers, 2004; Jonásová & Prach, 2004; Sauvard, 2007; Müller et al., 2008).

1.4 Fragestellung und Ergebnisse

1.4.1 Einfluss von Kronenschluss und unterschiedlichen Lücken- und Randlinienstrukturen auf das Vorkommen ausgewählter Insektengruppen (Artikel I)

Um den Einfluss unterschiedlich lichter Habitattypen auf die Biodiversität von ausgewählten Insektengruppen zu prüfen, wurden 2006 im Nationalpark Bayerischer Wald durch den Buchdrucker (*Ips typographus*) geschaffene Lücken mit künstlichen Waldrändern, Wiesen und geschlossenen Waldbeständen verglichen (Müller et al., 2007). In die Untersuchung einbezogen wurden xylobionte Käfer (Schmidl & Bußler, 2004), Wanzen, Bienen und Soziale Wespen. Der Fang erfolgte mit Flugfensterfallen während der Vegetationszeit an 12 räumlich getrennten Transekten entlang von Ökotonen an Innen- und Außensäumen von geschlossenen Beständen, in sechs „Buchdruckerlücken“ und an sechs künstlichen Waldrändern mit einem Übergang zu Wiesen.

Nachgewiesen werden konnten 204 xylobionte Käferarten (4.124 Ex.), 96 Wanzenarten (2.301 Ex.) und 65 Arten von Bienen und Sozialen Wespen (1.888 Ex.). Die Biodiversität und Abundanzen von Wanzen und von Bienen und Sozialen Wespen stieg signifikant vom geschlossenen Bestand zu lichteren Randbereichen an und erhöhte sich weiter in den Lücken an Innen- und Außensäumen. Die Individuenzahl der xylobionten Käferarten stieg ebenfalls signifikant vom geschlossenen Bestand zu den lichteren Bereichen, aber nur bei Ökotonen mit Buchdruckerlücken. Auch die Anzahl stark gefährdeter xylobionter Arten der Roten Liste gefährdeter Tiere Bayerns (Schmidl et al., 2003) erhöhte sich signifikant in den vom Buchdrucker geschaffenen Lücken. Eine Indikator-Arten-Analyse ergab 60 Arten, die statistisch signifikant eine der Habitattypen präferierten: 29 waren an Lücken gebunden, 24 bevorzugten Wiesen, drei waren charakteristisch für Ränder mit angrenzenden Wiesen, drei für Ränder von Borkenkäferlücken, nur eine Art war typisch für geschlossene Waldbestände. Die Ergebnisse zeigen, dass *Ips typographus* die meisten Kriterien als Schlüsselart erfüllt (Simberloff, 1998), vor allem für die Biodiversität in Nadel- und Nadelmischwäldern. Seine Rolle ist hier multifunktional: Bereitstellung von Brutsubstrat, Aufschluss des Substrats für Folgesiedler und Öffnung der Bestände (Licht, Wärme) mit nachfolgender Sukzession der Bodenflora und meist einer Erhöhung des Blütenangebots, von der eine Vielzahl blütenbesuchender Insekten profitiert.

1.4.2 Die Rolle von *Ips typographus* im Nationalpark Bayerischer Wald für die Biodiversität xylobionter Käferarten (Artikel II)

Um die Auswirkung von durch Buchdruckertätigkeit entstandenem Totholz und folgenden Bestandslücken und den Einfluss des Bestandsalters für die Artenvielfalt und die Abundanzen von xylobionten Käferarten (Schmidl & Bußler, 2004) zu untersuchen, wurden 2007 im Nationalpark Bayerischer Wald entlang von fünf Transekten auf 126 zufällig ausgewählten Probekreisen á 0,1 Hektar holzbesiedelnde Käferarten erfasst. 21 Probekreise befanden sich in Altwaldbeständen mit Uraltbäumen (> 400 Jahre), 52 Kreise in Totalschutzflächen und 53 Kreise in der Managementzone des Parks, in der eine Holzentnahme der Fichte bei Buchdruckerbefall erfolgte. Die Untersuchungsflächen lagen in Bergmischwaldgesellschaften und in Hochlagenfichtenwäldern. In den Probekreismittelpunkten wurden jeweils eine Flugfensterfalle (Finnischer Typ) und eine Barberfalle positioniert (Müller & Brandl, 2009). Ergänzend erfolgte auf jeder Probekreisfläche zeitnormierter Handfang für 45 Minuten über einen Zeitraum von drei Wochen bei konstanten Witterungsbedingungen.

Zwischen Managementflächen, Totalschutzflächen und Altwaldrelikten ergab sich ein klarer Unterschied hinsichtlich der Totholzmengen und ihrer Zusammensetzung. Die höchsten Totholzmengen (> 200 m^3 ha^{-1}) wurden in den Totalschutzflächen mit großflächigem Buchdruckerbefall festgestellt, wobei hier die Fichte die überwiegende Totholzmenge stellte. In den Altwald-Reliktbeständen setzte sich das Totholz, mit abnehmenden Anteilen, aus Fichte, Rot-Buche und Weiß-Tanne zusammen. Die durchschnittliche Totholzmenge lag bei 200 m^3 ha^{-1}. In den Buchdrucker-Managementflächen verblieben nur bis ca. 20 m^3 Totholz pro Hektar, überwiegend aber nur Stöcke und schwachdimensionierte Holzerntereste der Fichtenholzentnahme.

Der den Analysen zu Grunde liegende Datensatz umfasste 280 xylobionte Käferarten in 12.257 Individuen. Nachgewiesen werden konnte, dass mit steigenden Totholzmengen und zunehmender Kronenöffnung durch Buchdruckeraktivität die Individuenzahl von Generalisten, Nadelbaumspezialisten und von gefährdeten xylobionten Arten der Roten Liste Bayerns (Schmidl et al., 2003) anstieg. Laubwaldspezialisten waren positiv assoziiert mit der Menge an Laubtotholz (v.a. Rot-Buche), aber negativ korreliert mit einer zunehmenden Kronenöffnung. Eine Analyse der Umweltgradienten ergab, dass Kronenöffnung und Totholzmenge die bestimmenden Faktoren für die Zusammensetzung der Artengemeinschaften war. Als signifikante Schwellenwerte für einen Wechsel der Artenzusammensetzung wurden eine Kronenöffnung von 23 % (Konfidenzintervall 11-49 %) und eine Totholzmenge von 64 m^3 ha^{-1} (Konfidenzintervall 35-160 m^3 ha^{-1}) festgestellt. Stark gefährdete xylobionte Arten der Roten Liste Bayerns konnten als Indikatorarten für die

Qualität von dichten und lichten Waldbeständen verwendet werden, aber nur wenn gleichzeitig ein hohes Totholzangebot vorhanden war.

1.4.3 Einflussfaktoren auf die Abundanzen von Borkenkäferarten und auf ihre Einstufung als Forstschädlinge (Artikel III)

Das forstliche Monitoring von Borkenkäfern beschränkt sich heute überwiegend auf die Überwachung des Buchdruckers und des Kupferstechers in Fallensystemen unter Verwendung weitgehend selektiver Pheromone. *Ips typographus* und *Pityogenes chalcographus* sind aber nur zwei von mehr als 100 Borkenkäferarten in Mitteleuropa. Nur ein Drittel von ihnen wird als schädlich eingewertet (Lieutier et al., 2004). Warum manche Arten als schädlich gelten, andere nicht, ist unklar. Der Klimawandel könnte zu Wirtsbaumwechseln (Cudmore et al., 2010) und Interaktionen zwischen Borkenkäfern, Milben und Pilzen führen (Paine et al., 1997; Hofstetter et al., 2007), die zu einer anderen Einschätzung mancher Art hinsichtlich ihrer Schädlichkeit führen könnte. Ähnlich unbekannt sind die Gründe, warum manche Borkenkäferarten in den Wäldern Mitteleuropas häufig, andere selten sind und ob die häufigen auch die als schädlich eingestuften Arten sind.

Generell sind Verbreitung und Häufigkeit von phytophagen Insekten eng an die Verbreitung und Häufigkeit der Wirtspflanzen gebunden (Quinn et al., 1998). Stenöke Arten, die seltene Wirtspflanzen nutzen, müssen deshalb ebenfalls selten sein. Im Gegensatz dazu können polyphage Insekten, die weit verbreitete und häufige Wirtspflanzen nutzen, sowohl häufig wie auch selten sein. Die Wirtsbaumspezifität von Insekten hat sowohl eine phylogenetische wie eine ökologische Komponente (Kelly & Farell, 1998; Kergoat et al., 2005; Goßner et al., 2009). Dies impliziert zwei Vorhersagen. Erstens, die Abwehrstrategien von Wirtspflanzen sind oftmals konservativ und deshalb ähnlich, deshalb können Insekten auch nahe verwandte Wirte attackieren, ebenso jedoch phylogenetisch weit getrennte Familien, wenn sie ähnliche Abwehrstrategien besitzen (Berenbaum, 1995; Wiklund & Friberg, 2009). Zweitens, die Anzahl der Wirte wächst mit dem Verbreitungsareal des Käfers. Unabhängig davon muss davon ausgegangen werden, dass mit zunehmender Ressourcenverfügbarkeit (Angebot an Wirtsbäumen) die Abundanz von Arten ansteigt (Brändle & Brandl, 2001). Daraus ließe sich die Annahme ableiten, dass häufige Arten und schädliche Arten eine breite Wirtsspezifität aufweisen und häufige Wirte befallen.

Um die bestimmenden Größen für Abundanz und Schädlingseinschätzung von Borkenkäferarten in Mitteleuropa zu prüfen, wurden Daten über die Wirtspflanzen der Arten, die Verbreitung der Arten, die verfügbare Ressource der Arten, die Ernährungsstrategie, die Körpergröße und die Zahl der maximalen Generationen pro Jahr zusammengetragen. Die Abundanzen wurden auf der Basis von 1.793 quantitativen Flugfensterfallenfängen ermittelt,

ohne Verwendung attrahierender Komponenten (z.B. Ethanol, Pheromone). Insgesamt wurden 88 Arten in 308.298 Exemplaren erfasst. Die Fallenstandorte lagen vom Flachland bis in die hochmontanen Zonen von Bayern, Hessen, Baden-Württemberg, Tschechien und Zentral- und Südwestfrankreich. Die Arteigenschaften wurden für 109 Borkenkäferarten, die zweifelsfrei in Deutschland vorkommen, erfasst. Für alle Arten wurden die Wirtsbaumgattungen aus Literaturangaben u.a. Escherich (1923), Grüne (1979), Pfeffer (1995) und eigenen Quellen ermittelt. Weitere Angaben zur Verbreitung und Biologie der Arten wurden überwiegend von Schedl (1981), Köhler & Klausnitzer (1998), Böhme (2005) und aus eigenen Daten zusammengefasst.

Die Einwertung als „Pest species" folgt Grégoire & Evans (2004). Die Wirtsgattungs-Spezifität der Arten wurde mittels einer Phylogenie der Wirtspflanzen als „Root Phylogenetic Diversity Index" berechnet (Symons & Beccaloni, 1999). Dieser ermöglicht auch die Berücksichtigung von Arten mit nur einer Wirtspflanze. Da nicht über alle Borkenkäferarten Fallenfänge oder Ressourcendaten verfügbar waren und die wenigen Arten an krautigen Pflanzen eleminiert wurden, reduzierte sich die Zahl für die abschließenden Auswertungen auf 80 Arten. Die Phylogenie der Borkenkäferarten wurde auf der Grundlage von Cognato & Vogler (2001), Hunt et al. (2007), dem taxonomischen System (Grüne, 1979) und paläo-chronologischen Daten von Borkenkäfernachweisen aus fossilem Bernstein erstellt (Petrov & Perkovsky, 2008; Kirejtshuk, 2009; Kirejtshuk et al., 2009).

Die vier Arten mit der höchsten Anzahl an Wirtsgattungen waren mit 19 Gattungen *Xyleborus saxesenii* (Ratz.), mit 17 *Scolytus rugulosus* (Müll.), mit 16 *Xyleborus dispar* (F.) und mit 13 Gattungen *Scolytus mali* (Bechst.). Die höchste Abundanz im Datensatz hatte *Xyleborus saxesenii*. Die Adventivarten *Xyleborus germanus* und *Cyclorhipidion bodoanus* waren zwei der sechs häufigsten Arten. Vier Nadelholz-Gattungen erwiesen sich am artenreichsten, *Pinus* mit 59 Arten, *Picea* mit 38, *Abies* mit 22 und *Larix* mit 17 Arten. Bei den Laubhölzern sind *Quercus* mit 16 Arten, *Ulmus* mit 13, *Carpinus* mit 11 und *Fagus* mit 10 Arten die Wirtsbaumgattungen mit den meisten Borkenkäferarten.

Bei der Modellierung mittels eines Generalisierten Modells (Generalized least square Models), unter Berücksichtigung des Stammbaumes der Baumgattungen, zeigte Pagel's λ, dass die unterschiedlichen Artenzahlen an den Baumgattungen deutlich von der Wirtsphylogenie bestimmt werden. Unter Berücksichtigung der Phylogenie ergab sich, dass die beste Erklärung für die Anzahl von Borkenkäferarten an den Wirtspflanzen die Ressourcenverfügbarkeit ist, welche die Arten-Areal-Hypothese unterstützt (Strong et al., 1984; Brändle & Brandl, 2001). Damit folgen die Borkenkäfer dem allgemeinen Muster von phytophagen Arthropoden (Brändle & Brandl, 2001). Die Wirtsbaumspezifität der Borkenkäferarten (RootPD Index) war signifikant korreliert mit der Verbreitung der Borkenkäfer und signifikant höher für die xylomycetophagen Arten.

Mit Hilfe der gewählten Variablen konnte die Variabilität der Abundanz mit einem R^2 von 0,53 erklärt werden, dabei ergab sich kein phylogenetisches Signal für die Borkenkäferarten. Alle Variablen, mit Ausnahme der Anzahl maximaler Generation pro Jahr, ergaben signifikante unabhängige Erklärungsbeiträge. Wie erwartet, stiegen die Abundanzen mit der verfügbaren Ressource, der sinkenden Wirtsbaumspezifität, der Verbreitung der Borkenkäferarten und mit sinkender Körpergröße. Die Abundanzen der phloeophagen Arten waren niedriger als die der xylomycetophagen Arten. Damit wird die Abundanz in erster Linie durch ressourcenbezogene Variablen bestimmt.

Die Einwertung als Schädling konnte deutlich schlechter modelliert werden (R^2 = 0,25 Pestscore Europe, R^2 = 0,19 Pestscore central Europe). Signifikant relevant waren die artspezifischen Eigenschaften Körpergröße und maximale Zahl der Generationen pro Jahr. Dabei folgte die Körpergröße dem umgekehrten Trend wie bei der Abundanz. Schädlinge neigen dazu, größer zu sein als Nicht-Schädlinge. Dies kann damit begründet werden, dass größere Käferarten zu größeren und damit ökonomisch wertvolleren Hölzern tendieren, was ihre Schädlichkeit erhöht. Die Fähigkeit, mehrere Generationen im Jahr zu absolvieren, ermöglicht diesen Arten darüber hinaus bei hoher Ressourcenverfügbarkeit und unter günstigen Witterungsbedingungen, ihre Populationen rasch aufzubauen und damit große Flächen zu befallen.

1.5 Schlussfolgerungen

1. Borkenkäfergradationen sind im montanen und alpinen Nadelwaldbereich eine natürliche Erscheinung und viele Organismen, insbesondere auch gefährdete Arten der Roten Listen, profitieren von der steigenden Habitatdiversität, den Totholzmengen und der Erhöhung von Belichtung und Temperatur in durch Borkenkäfer verursachten Lücken und Totholzflächen.

2. Unter wirtschaftlichen Gesichtspunkten werden ungestörte Borkenkäfer-Massenvermehrungen auf Totalschutzflächen beschränkt bleiben. Gleichwohl sollten einzelne Lücken auch in bewirtschafteten Wäldern zugelassen werden, hiervon können eine Vielzahl waldbewohnender Insekten profitieren.

3. Um natürliche Störungen zu simulieren, sollten daher auch in Bergmischwäldern im mittleren Alter Lücken mit einem gewissen Totholzangebot geschaffen werden. Ein Auspflanzen der Flächen nach der Holznutzung sollte unterbleiben, um die Phase mit hoher Belichtung nicht zu verkürzen. Sie stellt in vielen Wäldern heute einen seltenen Habitattyp dar, insbesondere in den jungen und immer dichter werdenden Wirtschaftswäldern.

4. Im Bergmischwald und Hochlagenfichtenwald sind Kronenöffnung und Totholzmengen die entscheidenden Habitatparameter für die Artenvielfalt xylobionter Insekten. Gerade das Nebeneinander von sehr lichten und sehr dichten Bereichen fördert die Artenvielfalt. In dichten Beständen montaner Wälder mit weniger als 20 Prozent Kronenöffnung sollten sukzessive Totholzmengen von 30-60 m^3 ha^{-1} von Rot-Buche und Fichte mittelfristig angereichert werden. In offenen Beständen mit mehr als 20-50 Prozent Kronenöffnung sollte ein ähnlicher Totholzwert, aber überwiegend aus Nadelholzarten, angestrebt werden. Letzteres fördert sowohl Insekten, die auf Fichte spezialisiert sind, wie auch die Verjüngung der Fichte.

5. Die Häufigkeit von Borkenkäferarten lässt sich am besten durch Ressourcen bezogene Variablen erklären. Im Gegensatz dazu lässt sich die Einwertung einer Art als Schädling durch die artspezifischen Eigenschaften Körpergröße und maximale Zahl der Generationen pro Jahr erklären. Zwei der sechs häufigsten Arten in unseren Wäldern sind Adventivarten. Die Überwachung nur altbekannter Schädlinge vernachlässigt die mögliche Bedrohung durch eingeschleppte Arten, die im Zuge des Klimawandels relevant werden könnten. Neue Interaktionen von Borkenkäferarten, beispielsweise mit Pilzen, könnten dabei auch rasch die ökonomische Bedeutung von bisher wenig beachteten Arten verändern. Daher sollte beim forstlichen Monitoring ein breiteres Spektrum an Borkenkäferarten Berücksichtigung finden.

2 Summary

Scolytids have been studied more than any other forest insect group, but most investigations have been restricted to only a few species and mainly to their role as pests. The thesis here aimed to expand these studies to on the one hand the role of pest species as ecosystem engineers and thereby their influence on biodiversity and on the other hand to the whole family of Scolytinae to improve the understanding why some are abundant and some are rare as well why some species occur as pests and other do not. For a comparison of gaps generated by outbreaks of the spruce bark beetle (*Ips typographus*) on biodiversity in the area of the National Park ‘‘Bavarian Forest’’ with openings (e.g. meadows) created by humans insects were sampled using flight interception traps across twelve ecotones between edges of closed forest. The diversity and species density of true bugs, saproxylic beetles and of bees/wasps increased significantly from the closed stand to the edge, and continued to increase inside the openings particularly in gaps of bark beetles. 29 of the species preferred gaps, 24 preferred meadows, three were characteristic for edges of meadows, three for edges of bark beetle gaps, but only one was typical of closed forest. The results emphasize

the value of the policy of non-interference with natural processes pursued in some protected areas for conservation of insect diversity. From these results one can suggest that logging in recent gaps in medium aged mixed montane stands should aim at retention of a part of the dead wood. Planting should be avoided, to lengthen the important phase of sunlit conditions.

The analysis of increasing dead wood due to bark beetle infestation as well as tree senility bark beetle and further dead wood increasing processes was conducted on 126 plots with flight-interception traps, pitfall traps and direct search. Increasing amounts of spruce dead wood and opening of the canopy by bark beetles had positive effects on the abundance of host-generalist, conifer-specialist, and red-listed saproxylic beetles. Broadleaf specialists were positively associated with the amount of broadleaf dead wood and negatively associated with canopy openness. Gradient analysis of beetle assemblages revealed two major environmental axes: canopy openness and amount of dead wood. We found a threshold for community divergence at a canopy openness of 23% and at an amount of dead wood of 64 m^3 ha^{-1}. Critically endangered species served as indicators of dense and open forests, but only when the amount of dead wood was high. The results suggest that, to maintain saproxylic beetle assemblages, the amount of dead wood in commercial montane forests needs to be tripled, with a focus on broadleaf wood in dense stands and spruce wood in open stands. For large protected areas in Europe, our data suggest that bark beetle infestation and senescence without active forest management improves habitat conditions for saproxylic beetles.

The importance of variables on the abundance and pest classification of bark beetles was investigated by compiling data of 109 species occurring in Germany. Abundance was estimated by 1,793 passive flight-interception traps across central European forests (88 species, 308,298 specimens). Phylogeny was created for host genera as well as for bark beetle species. Host range was calculated as the root phylogenetic diversity index. The variation in the abundance of the scolytids was best and well-explained by resource-related parameters. In contrast to abundance, the pest classification could be explained by the species-specific traits body size and maximum number of generations, but the explained variance was lower. Two of the six most-abundant species were invasive and non-native. The implication of these results for monitoring are that a restriction to the few well-known, large pest species, may result in overlooking invading species and the possible ensuing alteration of forests ecosystems. However a consideration of invading species may particularly important with increasing global trade and the rapidly changing climate.

3 Literatur

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4 Anhang

Erklärung zu eigenen Beiträgen und Veröffentlichungen

Artikel I: Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P. 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. Biodiversity and Conservation 17, 2979-3001.

Die Idee für diesen Artikel stammt von J. Müller. Die Arterfassung im Gelände, die komplette Determination aus Hand- und Eklektorfängen und die ökologische Charakterisierung der xylobionten Käferarten wurden von mir vorgenommen. Die Bestimmung der Wanzenarten erfolgte durch M. Goßner, die der Bienen und Sozialen Wespen durch T. Rettelbach. J. Müller erstellte im Wesentlichen die statistischen Analysen und das vorläufige Manuskript. Die Artspezialisten überarbeiteten das Manuskript für ihren jeweiligen Spezialbereich. P. Duelli gab wertvolle Hinweise für die Endfassung des Artikels.

Artikel II: Müller, J., Noss, R.F., Bussler, H., Brandl, R. 2010. Learning from a „benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation 143, 2559-2569.

Die Idee für diesen Artikel stammt von J. Müller und mir. Die Arterfassung im Gelände, die komplette Determination aus Hand- und Eklektorfängen und die ökologische Charakterisierung der xylobionten Käferarten wurden von mir vorgenommen. J. Müller erstellte im Wesentlichen die statistischen Analysen. Das Manuskript wurde von mir und J. Müller verfasst. R. Brandl unterstützte die statistischen Auswertungen und korrigierte das Manuskript. R. F. Noss überarbeitete die Endfassung des Artikels.

Artikel III: Bussler, H., Bouget, C., Brustel, H., Brändle, M., Riedinger, V., Brandl, R., Müller, J. 2011. Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. Forest Ecology and Management 262, 1887-1894.

Die Idee für diesen Artikel stammt von mir. Ziel war es, verschiedene eigene Studien zur Borkenkäferfauna mit weiteren Daten aus Deutschland und Europa zu kompilieren. Die Datenerhebung, ihre Verifizierung und die Erstellung des Manuskriptentwurfs wurden im Wesentlichen von mir durchgeführt. C. Bouget und H. Brustel stellten die französischen Daten zur Verfügung. J. Müller half bei der statistischen Analyse, M. Brändle bei der

Erstellung des Stammbaums der Borkenkäferarten. Verena Riedinger eruierte die Genbanksequenzen der Pflanzengattungen. R. Brandl half bei der Erstellung des phylogenetischen Stammbaums der Wirtspflanzen, unterstützte die statistischen Auswertungen und korrigierte die Endfassung des Manuskripts.

Artikel IV: Bussler, H., Müller, J. 2004. Borkenkäferzönosen in wärmegetönten Eichenmischwäldern Nordbayerns – Bark beetle communities in oak-mixed-forests on warm stands in Northern Bavaria.- Forst und Holz 59, 175-178.

Idee und Konzeption für die Untersuchung stammen von mir und J. Müller. Die Arterfassung im Gelände und die Determination des gesamten Materials wurde von mir durchgeführt. Auswertung und Manuskripterstellung erfolgten durch mich. J. Müller überarbeitete die finale Fassung.

Artikel V: Bussler, H. 2006. Neue Borkenkäferarten in Bayern – Eine Gefahr für Laub- und Nadelbäume – New bark beetle species in Bavaria – danger to deciduous and coniferous trees. Jahrbuch der Baumpflege 2006, 107-112.

Der Artikel wurde von mir als Synopse verschiedener eigener Untersuchungen über adventive Borkenkäferarten in Bayern erstellt. Gleichzeitig handelt es sich um die schriftliche Fassung eines gleichnamigen Referats, das von mir im April 2006 in Augsburg, bei den Deutschen Baumpflegetagen gehalten wurde.

Artikel VI: Bußler, H., Schmidt, O. 2008. Remarks on the taxonomy, distribution and ecology of *Trypodendron laeve* Eggers, 1939 (Coleoptera: Scolytidae). Nachrichtenblatt bayerischer Entomologen 57, 62-65.

Der Artikel wurde von mir auf Grund mehrerer eigener Nachweise der relativ unbekannten Borkenkäferart verfasst. O. Schmidt war bei der Literaturrecherche behilflich und redigierte die Schlussfassung des Manuskripts.

Erklärung

Ich versichere, dass ich meine Dissertation "*Bark beetles – between pest species and ecosystem engineers*" selbständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Feuchtwangen, August 2011

Danksagung

Diese Dissertation ist Produkt einer seit 1968 andauernden „entomologischen Entdeckungsreise“, die als Sammler begann. Borkenkäfer sind bei Koleopterologen nicht sehr beliebt, meist klein, überwiegend braun oder schwarz und schwierig zu bestimmen. Ohne die Unterstützung durch Konrad Witzgall und Ulrich Bense hätte ich mir die Kenntnisse für eine sichere Determination von Borkenkäfern kaum aneignen können und mir wäre ihre faszinierende Biologie und Ökologie verborgen geblieben.

Ein Glücksfall war die kurze Zusammenarbeit mit Jörg Müller an der Bayerischen Landesanstalt für Wald und Forstwirtschaft in Freising, vor allem in Bezug auf Datenhaltung und Statistik. Gefördert wurde unsere Forschung durch Olaf Schmidt und Hans-Jürgen Gulder, ohne sie wäre diese fruchtbare Zusammenarbeit in Freising nicht möglich gewesen.

Hilfreiche Diskussionen und Kommentare zu Teilen meiner Arbeit lieferten Jürgen Schmidl, Volker Dorka, Markus Blaschke, Helge Walentowski, Petri Martikainen und Martin Goßner.

Ein herzlicher Dank gilt auch Jenny Berg, die mich bei der Dateneingabe unterstützte, und Sabine Bußler für die linguistische Durchsicht der Arbeit.

Mein besonderer Dank gilt Roland Brandl für die Betreuung meiner Arbeit und seine Unterstützung insbesondere in allen Statistikfragen.

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ORIGINAL PAPER

The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species

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Abstract The influence of natural disturbance on biodiversity is poorly known in the intensively cultivated landscape of Europe. As an example of insect disturbance we studied effects of gaps generated by outbreaks of the spruce bark beetle (*Ips typographus*) on biodiversity in the area of the National Park "Bavarian Forest" and compared them with openings (e.g. meadows) created by humans in these forests. Insects were sampled using flight interception traps across twelve ecotones between edges of closed forest, six bark beetle gaps and six meadows. The diversity and species density of true bugs and of bees/wasps increased significantly from the closed stand to the edge, and continued to increase inside the openings at interior and exterior edges. Species density in saproxylic beetles also increased significantly from closed forest to opening, but only across ecotones including bark beetle gaps. Similarly, the number of critically endangered saproxylic beetles increased significantly in bark beetle gaps. Using indicator species analysis a total of 60 species were identified as possessing a statistically significant value indicating preference for one of the habitat types along the ecotones: 29 of them preferred gaps, 24 preferred

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meadows, three were characteristic for edges of meadows, three for edges of bark beetle gaps, but only one was typical of closed forest. Most of our results support the thesis that *I. typographus* fulfils the majority of criteria for a keystone species, particularly that of maintenance of biodiversity in forests. Our results emphasize the value for the study and conservation of insect diversity of the policy of non-interference with natural processes pursued in some protected areas. As a recommendation to forest management for increasing insect diversity even in commercial forest, we suggest that logging in recent gaps in medium aged mixed montane stands should aim at retention of a part of the dead wood. Planting should be avoided, to lengthen the important phase of sunlit conditions.

Keywords Bark beetles · Forest edge · Gaps · Saproxylic beetles · True bugs · Bees and wasps · Insect outbreak

Introduction

After 5,000 years of civilisation history in Europe (Angelstam 1997; Grove 2002; Speight 1989), recorded experience on natural disturbance and its value for the maintenance of biodiversity is accordingly scarce. The majority of topics in conservation biology today deal with different conservation management practices in intensively used landscapes. However, the interest in natural, dynamic processes such as flooding (Dziock et al. 2006) or fire (Martikainen et al. 2006) and their influence on biodiversity is increasing. It is supposed that the understanding of natural dynamics is important for the development of suitable conservation management, even in an anthropogenic landscape. In forests, competition between humans and saproxylic beetles has a long history (Grove 2002). The European spruce bark beetle *Ips typographus* is considered to be the most serious pest species of mature spruce stands, mainly of Norway spruce, *Picea abies*, throughout Eurasia (Grodzki et al. 2004; Wermelinger 2004). Among all types of forest damage from 1950 to 2000 in Europe, 2–9 million m^3 per year of timber were destroyed by bark beetles, mainly *I. typographus* (Schelhaas et al. 2003). The preference of this species for mature spruce trees increases the economic impact of its damage. With regard to these facts it is not surprising that most published research on bark beetles deals with damage and prevention of outbreaks in commercial forests (Eriksson et al. 2006; Hedgren and Schroeder 2004; Reeve 1997; Wermelinger 2004). By contrast, some studies have pointed out the ecological value of *I. typographus* and other bark beetles as ecosystem engineers and so-called keystone species, driving forest regeneration, and producing snags and a rich patchiness in forest canopies (Jonášová and Pracha 2004; Martikainen et al. 1999). Apart from providing these ecosystem services, the arthropod complex associated with *I. typographus*, including more than 140 species (Weslien 1992), is in itself a significant contribution to diversity.

The ‘keystone species concept’, originally developed to describe the influence of a starfish’s predatory activities on “persistence and integrity” of a rocky intertidal community (Paine 1969), has been broadly applied over the years in ecology and conservation. Despite an ongoing debate about the validity of the concept, there is a growing consensus that a small subset of species can have a disproportionately large effect on ecosystems, compared to their abundance or biomass (Simberloff 1998). These keystone species are functionally linked to the persistence of an array of other species and play a critical role in the organization and/or functioning of the ecosystem. Mills et al. (1993) described five broad categories of keystone species, one of them being keystone habitat modifiers, also called ‘ecosystem engineers’ (Lawton and Jones 1995). The major changes in forest

structure, light regimes and increase in dead wood caused by *I. typographus* infestations in our study area are reasons for believing that this bark beetle plays the role of a keystone species in montane forests where spruce occurs in mixture or as the dominant tree species. The fact that *I. typographus* is alone amongst 35 bark beetle species in the study area in being able to kill larger numbers of mature Norway spruce trees indicates a low functional redundancy, integral to the concept of keystone species by Walker (1995).

The general importance for biodiversity of gaps in forests, especially windthrow gaps, is well known and demonstrated in numerous previous studies (Barbalat 1998; Fayt et al. 2006; Bouget and Duelli 2004). A general preference of many insects for forest edges exposed to the sun was revealed by studies at man-made forest edges adjacent to agricultural land (Duelli and Obrist 2003; Duelli et al. 2002a; Flückiger et al. 2002). Duelli (2006) even concluded that biodiversity of forests is concentrated mainly along their edges (Duelli 2006), and that what we usually call forest species are in fact mostly forest edge species (Wermelinger et al. 2007).

Before we can state that *I. typographus* is a keystone species, we have to show the high preference of other species for the habitat created by this bark beetle. To satisfy the criterion of low functional redundancy, this habitat should not be provided by other types of openings made by humans, such as meadows, which are also available in the montane zone.

Commercial forestry has in the past few centuries created dense and young forests throughout Europe. The current growing stock of European forests has a mean volume three times higher than in 1950 (Nilsson et al. 2001; Schelhaas et al. 2003), but large, old trees are rare (Hammond and Harding 1991; Speight 1989). There is also a lack of structural variation (patchiness) in our forests, caused by the rarity of gaps and interior edges. The immense alteration of natural processes involved in plantation forestry had a knock-on effect on the saproxylic fauna, with species becoming extinct or threatened by extinction (Müller et al. 2005a).

Natural openings in Central European forests are mostly gaps caused by windthrow or outbreaks of insect species such as bark beetles. In the National Park "Bavarian Forest" these kinds of events generally did not occur simultaneously in the past, but were nevertheless linked. Records of large scale windthrow events are available for approximately the last 130 years. However, a large bark beetle attack in the core zone, unaffected by management intervention for many years, offers the opportunity to study the influence of a natural disturbance process on biodiversity in a montane forest. This dramatic and rapid change to the forest induced a controversial discussion on policy throughout the region. The question "What are the ecological consequences of 'wilding' (that is, non-interference with natural processes) as a long-term conservation strategy?" was intensively discussed in the region, as also in many other European countries. The question was identified as one of the 100 most important ecological problems of high policy relevance in the UK (Sutherland et al. 2006). Hence, it is important to study natural processes which lead to changing habitat conditions in strictly protected forested areas, especially where such processes are controversial with respect to their effect on our carefully managed landscape.

Heavy bark beetle infestation creates openings in forest where non-interference may be practiced, as one management option. To assess the effects of this "opening-up" process on biodiversity and compare it to man-made openings, such as meadows, we studied assemblages of three species-rich insect groups, which include typical forest insects (saproxylic beetles, true bugs and wasps/bees) along ecotones from gaps/meadows, across interior/exterior edges into closed forest, in the montane-mixed forest zone. To assess the role of *I. typographus* as a keystone species in a forested montane landscape, this project addressed the following questions:

1. Does species density and diversity alter along a horizontal transect across bark beetle gaps, forest edges and closed forest?
2. Does the diversity pattern along ecotones from bark beetle gaps to closed forest differ from ecotones from meadows into the forest, therefore allowing a low functional redundancy for *I. typograhus* to be stated?
3. Do habitat preferences of species for gaps, meadows, exterior and interior edges, and closed stands support the keystone hypothesis?
4. Is species density in tree crowns similar to that near ground level in open areas, and therefore a suitable alternative habitat for sun-loving species, even in dense forests?

Materials and methods

Study area

The study was carried out in the National Park "Bavarian Forest", a 24,000 ha mountainous region in South-eastern Germany (Fig. 1). Average daily temperatures range from 3.5 to 6.5°C with an average annual precipitation of 1,100–1,500 mm. The mean duration of snow cover is about 5–6 months in the zone studied; the vegetation period is 184 days. In contrast to the majority of German landscapes, the forested area of the National Park was settled late by humans, in the 15/16th centuries (Strobl and Haug 1993). Up to now, settlements were restricted to small clearings in the forest landscape. In the first 300 years of settlement, glassworks were responsible for most harvesting of wood. Despite a partly intensive logging in their immediate surroundings, the natural tree species composition was little affected. Furthermore, at the end of this period in 1850 stands of virgin forest still existed, especially in the upper montane zones. Within several decades in the late 19th and early 20th century, modern forestry altered tree species composition by the planting of mainly spruce after shelterwood logging and on areas windthrown or killed by bark beetles. In 1970 the first

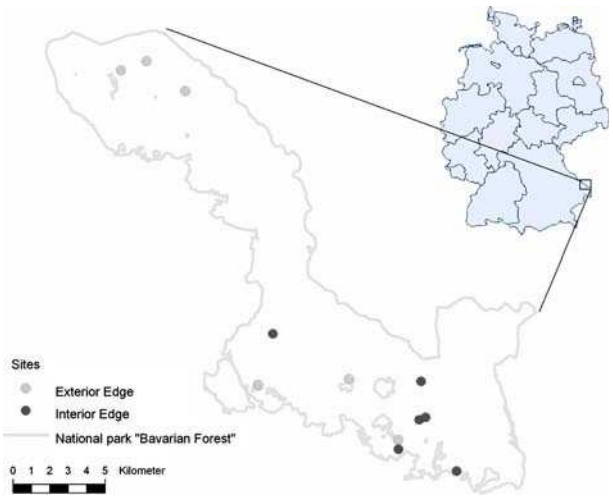

Fig. 1 Study area National Park "Bavarian Forest". The distribution of the 12 investigated transects across forest edges are shown. For more details see Müller et al. (2007a)

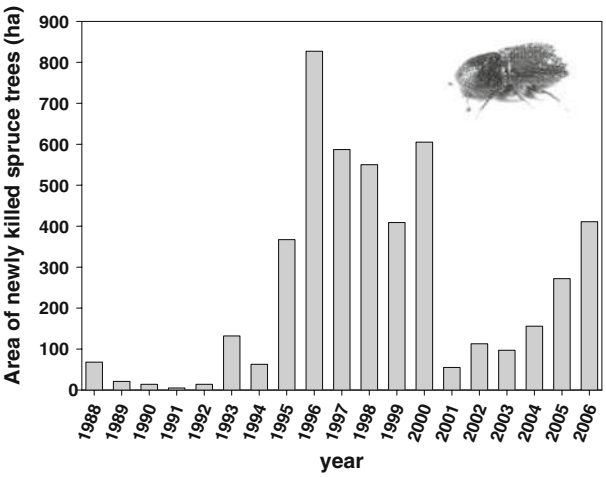

Fig. 2 Yearly area of newly infested spruce trees in hectares, mainly by European bark beetle *Ips typographus*, in the area of the National Park "Bavarian Forest" (in total 20% of the area)

National Park in Germany was founded in this area, resulting in a phasing-out in the core area of the Park of all logging activities. Today, the lower montane zones are dominated by mixed stands of mainly spruce *Picea abies*, beech *Fagus sylvatica* and a low percentage of silver fir *Abies alba*, while in the upper montane zone (>1,162 m) stands of *P. abies* still dominate, as in the time before human interference. Disturbances in this montane forest are older than modern forestry, introduced in the late 19th century. Historical sources report on destruction of forest in 1786 by windthrow and in 1796 by bark beetle. In the 19th century eight windthrows are recorded caused by severe storms in 1868 and 1870, followed by an extensive bark beetle outbreak in the subsequent years, especially in the virgin forests at higher altitudes (Strobl and Haug 1993). This seems similar to the process at present underway (Fig. 2). In old literature, it is remarked that even in untouched virgin forest, gaps caused by windthrow and bark beetle infestation, with huge amounts of standing and lying dead trees are regularly found (Hennevogel 1905). This indicates that disturbance by storm and bark beetle occurs naturally and widely in this montane forest ecosystem (Elling et al. 1987). Induced by several storms in the 1980s and a succession of hot summers in the 1990s, a large outbreak of *I. typographus* started, first with large areas of infestation at higher elevations, later at lower altitudes through the whole mixed montane zone (Fig. 2). This process has operated entirely without interference, because of the policy of no pest management followed in the core zone of the National Park. From an ecological point of view, a highly diverse pattern of patchiness with glades was created, especially in the mixed montane zone, containing forest plants and huge amounts of dead wood. The boundaries between gaps and closed forest represent a widely spread system of interior edges. In contrast, as a result of settlement history within the NP, some exclaves comprising meadows and former pastures exist. Edges of these features are distinguished below as exterior edges. They are dominated by plants of meadows and pastures.

Sampling transects

We selected 12 widely separated sites (Fig. 1): six at interior and six at exterior forest edges (for details see Müller et al. 2007a). The year of infestation of the six bark beetle gaps studied varied from 1993 to 2003. Investigated gaps and man-made openings were similar in size (bark beetle gaps 1.1–13.8 ha, mean 6.8 ha; meadows 0.5–12.0 ha, mean 6.5 ha), and

altitude (gaps, mean 897 m; meadows, mean 908 m). Until now, bark beetle attack has been concentrated in the South-East of the NP. Therefore the sites with interior edges were located mostly in this part of the area. Because stand structures are similar throughout the whole of the NP, the three exterior edges in the North-West are directly comparable with the other studied edges. On each ecotone we installed five traps. The first was placed in the gap or on the meadow, 40–70 m distant from the last tree at the edge, 1.5 m above the ground; the second at the last shrub or tree on the edge, also 1.5 m above the ground; the third installed with aid of a crossbow in the crown of the last tree at the edge at a height of 15–25 m, depending on the tree height; the fourth placed similarly in a tree crown in the forest interior, 60–80 m distant from the edge; the fifth under this tree, 1.5 m above ground. The distance of the last trap from the edge seems to us to be sufficient, according to previous studies on edge effects (Grimbacher et al. 2006; Wermelinger et al. 2007). To avoid sampling bias caused by differences in insect species density on the different tree genera *Picea*, *Abies*, *Fagus* and *Acer* we selected an equal number of deciduous trees for sampling in the exterior and interior edge categories as well as in the closed forest. All transects were located in mixed stands of deciduous and coniferous tree species. We did not measure habitat variables such as the amount of dead wood or the availability of inflorescences, but in all cases the amount of dead wood was higher in the bark beetle gaps, and inflorescences were more abundant in the open areas than in surrounding closed forests. For testing preferences at the species level we used the following five habitat types: opening/gap, interior/exterior edge, closed forest. To assess vertically differentiated preferences, we compared samples from canopy traps with those of strata nearer ground level.

Sampling of insects

Insects were sampled during 2006 using flight interception traps as a standardised method. This is one of the most frequently used methods for sampling beetles and true bugs in comparative studies of forests under different types of management (Basset et al. 1997; Grimbacher et al. 2006; Grove 2000; Kaila et al. 1994; Martikainen et al. 2000) and has also proved suitable for sampling bees and wasps (Müller et al. 2005b). Similarly to other types of traps, such as pitfall or Malaise traps, flight interception traps measure insect activity, with more individuals sampled at sites with higher activity. However, the higher activity in the species of our study is clearly related to availability of better quality habitats for mating, egg laying or feeding (Bense 1995). Therefore, we followed this widely used approach (Hyvärinen et al. 2006; Similä et al. 2003), already successfully applied in edge studies (Grimbacher et al. 2006), to compare species density in different types of stands. Traps consisted of a crossed pair of transparent plastic shields (40 × 60 cm) with a funnel of smooth plastic material attached to the bottom and a plastic roof at the top. To attract species searching for flowers, a yellow, adhesive tape was applied to one of the shields. At the end of the funnel a 1 l sampling jar filled with killing and preserving agent (1.5% copper-vitriol-solution) was mounted. The traps operated during the whole growth period of 5 months and were emptied each month (May–September) by filtering the collecting fluid through a tea strainer and transferring the catch to 70% ethanol.

Species included in the study

We focused our study on three taxonomic groups of insects: (I) saproxylic beetles (Coleoptera), which are dependent, during some part of their life cycle, upon dead or dying wood of moribund or dead trees (standing and fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics (Schmidl and Bußler 2004; Speight 1989). Highly

endangered species were only represented in this group, according to the red data book for Bavaria (Schmidl et al. 2003). (II) True bugs (Heteroptera) are primarily plant-sap feeders and/or predators. (III) Bees and social wasps (part of the Hymenoptera Aculeata) are typical visitors at inflorescences.

All specimens of the investigated groups were determined to species level. Determination was done by the authors, who are specialists for their groups, using the following literature: Coleoptera, HB (Freude et al. 1964–1983), Heteroptera, MG (Péricart 1972, 1983, 1987, 1998), TR (Osten 2000; Schmid-Egger and Wolf 1992; Westrich 1989). Reference specimens are deposited in the Bavarian State Collection of Zoology (ZSM), Munich. The complete list of species determined was published in Müller et al. (2007a). Based on this data, we calculated as response variables the species density as represented by the number of species per trap (Gotelli and Colwell 2001) and the diversity using the Shannon-Index (Magurran 1988) per trap.

Statistical analysis

To analyse the data across the three categories of opening (gap/meadow), edge and forest on each transect, we used the single trap in the opening and the two traps each at the edge and in the forest. This is an unbalanced sample design. Due to this fact, the global hypothesis of independence between the three spatial zones across the forest edges (gap/meadow, forest edge, closed forest), and the comparison of the spatial zones of the two types of edges (transect across interior and exterior forest edge) and each of the response variables were assessed by means of resampling-based multiple testing (Westfall and Young 1993). This nonparametric procedure allows for inferences to be made without imposing distributional assumptions, like normality or homoscedasticity, on the data. The situation is typical for insect trap data. The *P*-values obtained by this procedure were adjusted for multiple comparisons utilizing a step-down max-T approach (Algorithm 2.8 in Westfall and Young 1993), which ensures high power of the test procedure while controlling its family-wise error rate. For each response variable (species density, diversity), a post-hoc test (Tukey all-pair comparisons) was additionally applied to assess the differences in the rank transformed response variables between each pair of categories (Hothorn et al. 2006). The statistical analysis is based on implementations of the above procedures in the add-on package "coin" (Hothorn and Hornik 2005) within the R system for statistical computing (version 2.4.1, R Development Core Team 2006). To detect and describe the value of different species for indicating environmental conditions in the spatial categories (horizontal: gap/meadow, interior edge/exterior edge, closed forest; vertical: near forest floor, canopy) we used the Indicator Species Analysis (Dufrêne and Legendre 1997). This method produces an indicator value (IV) for each species by combining information on the concentration of species abundance in a particular category and the faithfulness of occurrence of a species in a particular category. It produces indicator values for each species in each category, which are tested for statistical significance using a Monte Carlo technique. Only species with a *P*-value <0.05 were accepted as indicator species. Species diversity was calculated using the Shannon Index. For both analyses PCORD 4.0 was used (McCune and Mefford 1999).

Results

Analysis was based on a total of 365 species: 204 saproxylic beetles (4,124 specimens), 96 true bugs (2,301 specimens) and 65 bees and social wasps (1,888 specimens).

Distribution of species density and diversity across horizontal transect

The species density of saproxylic beetles increased significantly across the interior edges, from closed forest to the opening (bark beetle gap). Across the exterior edges, species density did not differ between edge and opening (meadow), but in both it was significantly higher than in closed forest. For true bugs and bees/wasps (Fig. 3) the increase of species density across interior and exterior edges from closed forest to edge and openings was significant and similar in both types of edges, but the difference between edges and openings was not significant.

The Shannon Index applied to saproxylic beetles revealed no significant difference between the three types of zone across the horizontal transect (Fig. 3). Diversity of true bugs was higher in interior gaps than at their edges or in closed forest, and at exterior edge sites significantly higher in meadows than in closed forest. For bees/wasps the diversity was significantly higher at the edges and openings, for both types of forest edges, compared to the closed forest (Fig. 3).

The trends of an increase of species density and diversity were very similar across interior edges caused by bark beetle and exterior edges caused by humans (Fig. 3), with one exception. However, the increase of species density of saproxylic beetles from forest to opening was significant only for the bark beetle gaps, but not for the meadows. This is also true for the critically endangered saproxylic beetles. We found significantly higher numbers of specimens only in bark beetle gaps (Fig. 4).

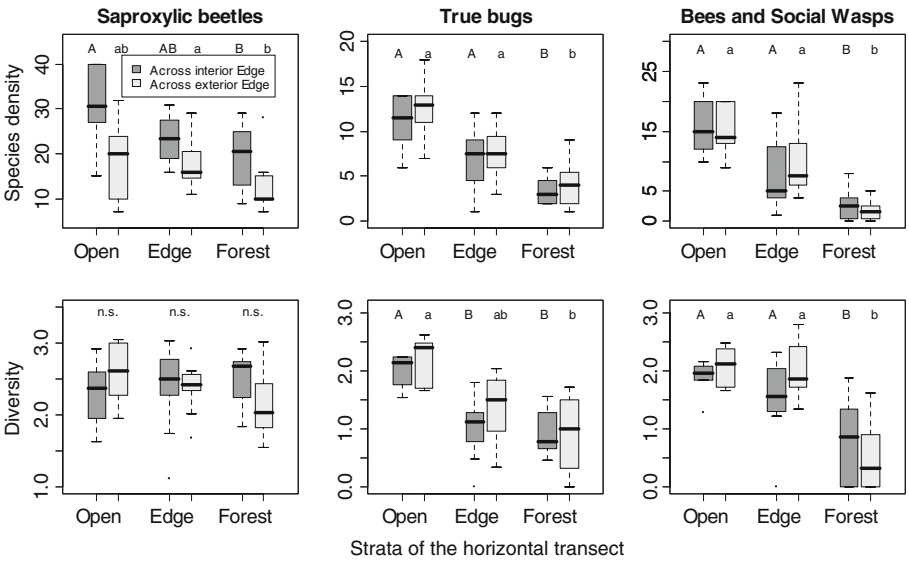

Fig. 3 Species density and diversity (median) of three groups of insects along a horizontal transect across interior forest edges (dark grey), open (gap), forest edge, and closed forest and across exterior edges (pale grey) with open (meadow), forest edge and closed forest. The two types of transects were tested separately (number of traps per transect type: open 6, edge 12, forest 12), as marked with lower- and upper-case characters. Different letters indicate significance of Tukey post-hoc tests, non significance is indicated by n.s.

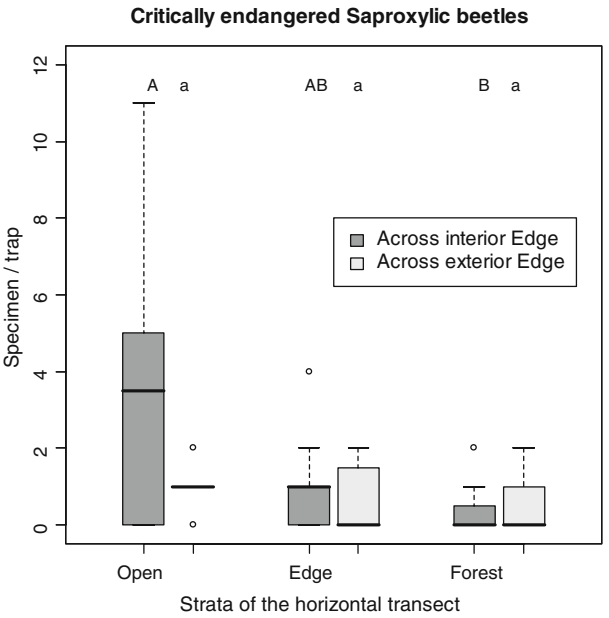

Fig. 4 Specimens (median) of critically endangered species per trap (RL Bavaria 2003 (Schmidl et al. 2003). Categories: least concern, endangered, critically endangered) along the horizontal transect across forest edges. The three categories were tested separately across interior and exterior edges, as marked with lower and upper-cased characters. For a detailed species list see Müller et al. (2007a)

Habitat preference of species

Using indicator species analysis, 60 insect species showed a significant indicator value for one of the five horizontal habitat types (Table 1). Most of these species (29) preferred the bark beetle gaps in forests, followed by the meadows (24 characteristic species). Three species each preferred exterior or interior edges, but only one the closed forest. The number of characteristic species varied among the three taxonomic groups. For saproxylic beetles, gaps (11 species) seem to be most important, but several species were characteristic for meadows (7 species). Two species could be identified as characteristic for exterior edges and five for interior edges. Only one species was found to prefer closed forests. Among the true bugs, species with significant indicator values could only be found for gaps (4) and meadows (9). Within the bees and social wasps the number of indicator species was highest in forest gaps (12), followed by meadows (8), whereas only one species showed a preference for exterior edges, and none could be found for the other strata.

Comparing strata at tree crown and near forest floor levels (Table 1) we found 4 saproxylic beetles characteristic for the canopy, but 13 at ground level. Among the true bugs seven species, mostly specialised on a particular tree genus (Table 1), were typical for the canopy, and only one for the stratum near ground level. Within the bees and social wasps no species was found to be typical for the canopy, but seven species were characteristic for the lower stratum.

Discussion

Species depending on particular zones

Along the ecotones from opening to forest we found in all three taxonomic groups a high number of species with a preference for gaps and meadows. Even if accompanying

Table 1 Preference of single species for a zone/stratum of the horizontal and vertical transects, using indicator species analysis (IV = indicator value, $P = P$-value) (Dufrêne and Legendre 1997)

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	*P*	Canopy	Forest ground	IV	*P*	Biology
Number of traps	6	12	6	12	24			24	36			
Coleoptera												
Anthaxia quadripunctata	**3**	2	1			38.6	0.007	1	5			Larva xyloph. in fresh CWD, adults on flowers
Tritoma bipustulata	**10**	2		1		35.6	0.018	1	12			Larva mycetophagouse on wood inhabiting fungi
Gaurotes virginea	**4**	3	5	3		30	0.036	2	13			Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
Curtimorda maculosa	**2**		1			28.2	0.033		3			Larva xylo-mycetoph. in advanced decomposed CWD
Mordella holomelaena	**3**		2			25.7	0.041		5			Larva xylo-mycetoph. in advanced decomposed CWD
Leperisinus fraxini	**2**	2			2	24.6	0.044	3	3			Larva xyloph. in fresh CWD
Scaphisoma agaricinum	**2**		2			21.8	0.048		4			Larva mycetophagouse on wood inhabiting fungi
Ischnomera caerulea		**6**				25	0.04	5	1			Larva xylophagouse in advanced decomposed CWD
Tillus elongatus		**13**				25	0.038	11	2			Larva zoophagouse (Scolytidae) in advanced decomposed CWD
Stenurella melanura	9	4	**181**	5	2	92	0.001		**201**	51.4	0.001	Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
Pityogenes chalcographus	13	74	**398**	164	76	72.2	0.004	87	**638**	66.7	0.022	Larva xyloph. in fresh CWD
Judolia sexmaculata			**10**	2		60.6	0.001		12			Larva xylophagouse in advanc. Decompos. CWD, adults on flowers

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	*P*	Canopy	Forest ground	IV	*P*	Biology
Lepturobosca virens			**18**			50	0.001		18			Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
Ampedus nigrinus	1	17	**155**	309	12	48.1	0.027	311	183			Larva xylophagouse in advanced decomposed CWD
Nudobius lentus		1	**6**			46.2	0.002		7			Larva zoophagous in fresh CWD
Pachytodes cerambyciformis	1		**10**	3		39.4	0.017		14			Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
Crypturgus hispidulus		1	**5**	3	4	31.2	0.034	5	8			Larva xyloph. in fresh CWD
Anobium pertinax		1	**8**		1	30.5	0.018		10			Larva xylophagouse in advanced decomposed CWD
Crypturgus cinereus		1	**3**	1	4	30	0.032	2	7			Larva xyloph. in fresh CWD
Malthodes hexacanthus			**7**	9	4	28	0.043	2	18			Larva zoophagouse in advanced decomposed CWD
Dasytes niger	1		**7**			28.5	0.02		8			Larva zoophagouse in advanced decomposed CWD
Leptusa pulchella			**2**	1		26.7	0.042		3			Larva zoophagouse in advanced decomposed CWD
Dasytes obscurus	1	3	32	**39**	1	58.8	0.002	28	48			Larva zoophagouse in advanced decomposed CWD
Ampedus erythrogonus	1	5	4	**32**	7	36.7	0.039	35	14			Larva xylophagouse in advanced decomposed CWD
Aplocnemus tarsalis		2		**10**		34.7	0.012	6	6			Larva zoophagouse in advanced decomposed CWD
Hedobia imperialis		2	1	2	**31**	42.1	0.009	18	18			Larva xylophagouse in advanced decomposed CWD
Polygraphus poligraphus	3	17	1	45	38			**76**	28	53.2	0.002	Larva xyloph. in fresh CWD

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	*P*	Canopy	Forest ground	IV	*P*	Biology
Ernobius abietinus		6		3	2			**11**		20.8	0.009	Larva xylophagouse in advanced decomposed CWD
Anaspis thoracica		1	1	26	2			**28**	2	19.9	0.043	Larva xylo-zoophagouse in advanced decomposed CWD
Aplocnemus nigricornis		1		5				**6**		16.7	0.026	Larva zoophagouse in advanced decomposed CWD
Hylastes cunicularius	1	15	7	10	58			6	**85**	54.4	0.002	Larva xyloph. in fresh CWD
Dasytes plumbeus	26	39	14	10	4			11	**82**	45.4	0.01	Larva zoophagouse in advanced decomposed CWD
Xyloterus lineatus	1	5	6	8	34			5	**49**	39.8	0.014	Larva mycetoph.in fresh CWD
Platycerus caprea	1	10	4	5	13			4	**29**	38.1	0.006	Larva xylophagouse in advanc. Decompos. CWD
Cychramus variegatus	1	3	6	11	11			1	**31**	35.5	0.007	Larva mycetoph. on woodinhabiting fungi
Dryocoetes autographus		3	14	5	28			3	**47**	28.8	0.032	Larva xyloph. in fresh CWD
Xyloterus domesticus	1	2	3		31				**37**	28.6	0.008	Larva mycetoph. in fresh CWD
Rhagium mordax	5	10	4	2	8			2	**27**	28.4	0.034	Larva xyloph. in fresh CWD, adults on flowers
Hylecoetus dermestoides	1	4	2	1	39				**47**	25.7	0.015	Larva xylo-mycetoph. in fresh CWD
Pteryngium crenatum		1	6	7	4			1	**17**	23.7	0.03	Larva mycetophagouse on wood inhabiting fungi
Bibloporus bicolor		1	1	3	3				**8**	20	0.03	Larva zoophagouse in advanced decomposed CWD
Heteroptera												
Orthops kalmii	**3**			1		52.7	0.001		4			Herbivorous, mostly on Apiaceae
Megalonotus chiragra	**2**					40	0.006		2			Mostly open area habitats, polyphagous, fruit-eating

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	*P*	Canopy	Forest ground	IV	*P*	Biology
Rhyparochromus pini	**2**					40	0.008		2			Open area habitats, polyphagous, fruit-eating
Plagiognathus arbustorum	**7**	1				37.8	0.014		8			Succession sites, zoo-herbivorous
Carpocoris purpureipennis	**10**		3			32	0.02		13			Open area habitats, herbivorous herbaceous plants
Leptopterna dolobrata	**2**	2				28.2	0.029		4			Open area habitats, herbivorous Poaceae
Saldula orthochila	**2**		1			28.2	0.028		3			Shores, Zoophagous
Tingis pilosa	**2**	1		1		28.2	0.015		4			Open forests, herbivorous on Lamiaceae
Lygus gemellatus	**2**	1	1			24.6	0.044		4			Open area habitats, herbivorous Artemisia
Palomena prasina	1		**29**	5		73.9	0.001	3	32			Herbivorous, arboricolous
Dolycoris baccarum	30	2	**56**	33		51.1	0.007	4	**117**	40.8	0.003	Herbivorous, arboricolous
Dictyla convergens			**7**			33.3	0.016		7			Herbivorous on Myosotis
Orius minutus			**2**			30.8	0.027		2			Zoophagous, mostly on Aphidina
Cremnocephalus alpestris	12	266	2	474	263			**981**	36	77.2	0.001	Coniferous trees, zoo-herbivorous, feeds on Aphidinae
Pentatoma rufipes	2	96	5	52	29			**154**	30	69.8	0.001	Deciduous and coniferous trees, zoo-herbivorous
Psallus varians	4	94	12	205	126			**367**	74	62.2	0.022	Deciduous trees, zoo-herbivorous, Fagaceae
Atractotomus magnicornis	1	9	1	7	6			**19**	5	31.8	0.011	Coniferous trees, zoo-herbivorous, feeds on Aphidinae
Phytocoris dimidiatus		2		5	15			**19**	3	30.1	0.005	Deciduous and coniferous trees, zoo-herbivorous

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	*P*	Canopy	Forest ground	IV	*P*	Biology
Acompocoris alpinus		3		2	1			**6**		16.7	0.03	Coniferous trees, zoophagous on Aphidinae
Dichrooscytus intermedius		6		3				**9**		16.7	0.022	Coniferous trees, herbivorous
Aculeata												
Bombus pascuorum	**52**	18	42	23	7	49.3	0.007	10	**132**	56.6	0.001	Open areas, polylectic
Andrena helvola	**9**	11	1		2	48.5	0.004	1	**22**	26.8	0.021	Open areas, forest edges, Asteraceae, Grossulariaceae, Liliaceae, Rhamnaceae, Rosaceae
Bombus lucorum	**99**	43	108	25	6	45.3	0.042	34	**247**	54.7	0.021	Open areas, open forests, meadows, polylectic
Dolichovespula norwegica	**5**	8			2	34.3	0.022	6	9			Montaine forests, nest by wood
Bombus hypnorum	**2**			1		33.1	0.015	1	2			Open forests, forest edges, polylectic
Vespula rufa	**6**		2	2		28.2	0.036	2	8			Open areas
Andrena haemorrhoa	**10**	6	2		1	27.8	0.049	1	18			Open areas, forest edges, polylectic
Dolichovespula sylvestris	**2**				1	18.1	0.034		3			Forests, open area, nectar feeder
Vespula vulgaris	3	**16**	1	1	3	43.3	0.013	6	18			Open areas
Apis mellifera	44	9	**386**	71	26	79.5	0.004	39	**497**	69.2	0.003	Honey bee
Hylaeus confusus	3	4	**33**	14	5	58.7	0.002	14	45			Forests edges, succession sites, wood-inhabiting in beetle galleries and Rubus, polylectic
Andrena lapponica	5	25	**74**	60	16	58.5	0.003	63	117			Boreo-montane, oligolectic, spezialised on Vaccinium
Bombus bohemicus	45	17	**88**	7	9	56.3	0.011	15	**151**	44.9	0.015	Cuckoo on *B. lucorum*, Taraxacum, Centaurea, polylectic

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	*P*	Canopy	Forest ground	IV	*P*	Biology
Bombus sylvestris	8	5	**29**	8	4	52.4	0.008	7	**47**	39.9	0.019	Cuckoo on *B. pratorum*, Taraxacum, Knautia, Centaurea
Bombus pratorum	7	9	**30**	13	17	46.6	0.013	24	52			Open forests, meadows, polylectic
Bombus hortorum	2		**5**			45	0.001		7			Forest edges and attached meadows, gardens, polylectic
Lasioglossum rufitarse		2	**13**	13		42.3	0.014	4	24			Montane species, forest edges, polylectic
Lasioglossum subfulvicorne	1	4	**14**	14	1	38.2	0.03	2	**32**	31.4	0.022	Forest gaps and edges, polylectic
Bombus jonellus	3	7	**11**	13		37.3	0.024	16	18			Open areas, mires, heath, polylectic
Lasioglossum lativentre	6	6	**10**	7		35.2	0.027	8	21			Forest edges, succession sites, polylectic
Hylaeus annulatus			**2**			33.3	0.017		2			Montane species, forests, wood-inhabiting
Sum of signif. species	24	3	29	3	1			12	22			

All specimens per habitat category are given, for species with $P < 0.05$ the *P*-values are given. The category is indicated by number of specimens in bold face. Species are arranged according to their preference for horizontal categories. The number of traps per category is also shown. CWD = coarse woody debris

environmental factors were not measured in present study, current studies (Müller, unpubl. data) in the same area prove that highest density of flowers occurs in gaps and meadows and the highest amount of dead wood in the bark beetle gaps. Moreover, the determinants for individual species can be validly discussed using existing knowledge. Most adults of the saproxylic beetles and Aculeata with a preference for openings are typical blossom visitors (Table 1). We explain the preference of other saproxylic species (e.g. *Ampedus auripes*, *Anobium pertinax*, *Leptusa pulchella*, *Malthodes hexacanthus*, *Nudobius lentus*) for gaps by a higher diversity and availability of dead wood structures. The volatiles emitted by recently dead and dying wood attract several species of Scolytidae, such as *Pityogenes chalcographus*, *Crypturgus cinereus*, *C. hispidulus* (Bußler and Müller 2004; Rohde et al. 1996). Of the blossom visitors without a connection to dead wood, the bees *Andrena haemorrhoa*, *A. helvola*, *Bombus hypnorum*, *B. lucorum*, *B. pascuorum* and the wasps *Dolichovespula norwegica*, *D. sylvestris*, *Vespula rufa* showed a preference for meadows, whilst the bees *Andrena lapponica*, *Apis mellifera*, *Bombus bohemicus*, *B. hortorum*, *B. jonellus*, *B. pratorum*, *B. sylvestris*, *Lasioglossum lativentre*, *L. rufitarse*, *L. subfulvicorne* preferred gaps. This agrees with other studies of Aculeata in forest openings (Flückinger 1999; Kuhlmann 2000).

Among the true bugs those species with a preference for meadows (Table 1) are typical inhabitants of open habitats. They feed on plants characteristic of ruderal and successional areas. Species with a preference for gaps are more typically associated with woodland or forest, as are the at least partly arboricolous *Dolycoris baccarum* and *Palomena prasina*. Previously published results report open areas and edges in forests to be preferred to closed stands by many other groups of arthropods, e.g. ground beetles (Carabidae) (Bedford and Usher 1994; Grove and Yaxley 2005), sawflies (Symphyta) (Flückinger 1999), flies (Diptera) (Bächli et al. 2006), hoverflies (Syrphidae) (Fayt et al. 2006), neuropterans (Neuroptera) (Duelli et al. 2002a) and spiders (Araneae) (Flückinger 1999).

There are several explanations for why the number of species with a preference for closed forest was low in the present study: firstly, our studied taxa are all insects, whose activity is more or less positively related to temperature, which is higher in openings than closed forest. Studies on insects restricted to closed canopies, or the interior of forests, are lacking in Central Europe. Additionally, most forest-dwelling insects are more strongly influenced by structural features such as dead wood colonized by fungi (Jonsell et al. 1999; Ódor et al. 2006), than by canopy cover, where these have not been attacked by bark beetles, the mature, formerly commercially managed stands of our study area possess a poor variety of lower vegetation, fungi and dead wood structures. However, we have to keep in mind that in old-growth beech forests a high diversity of dead wood structures can also be found in closed stands (Christensen et al. 2005), together with a rich saproxylic fauna (Müller et al. 2007b). Among taxa other than the insect groups studied here, such as birds, bryophytes or lichens, several species are well known to be strongly associated with closed stands (Nilsson et al. 1995; Saetersdal et al. 2004). A further reason for the absence in the present study of species characteristic of closed forest is the history of settlement in Europe, involving an extensive alteration of forest in all areas by clearance or intensive logging. Thus, those species strictly associated with large, unlogged forest landscapes must be expected to have become extinct centuries ago in all but a very few regions (Müller et al. 2005a; Speight 1989). Studies in forested areas with large old-growth stands do in fact report even on beetle species characteristic of the forest interior (Grove and Yaxley 2005).

Gaps versus meadows

For all taxa, our results showed higher species density only in bark beetle gaps. Additionally, we found species with significant value as indicators for either gaps or meadows. In general, open habitats in forests are patches in a shifting mosaic, whose inhabitants are open habitat generalists, forest edge or glade specialists, but also multi-habitat species which need both tree-covered and open habitats in order to complete their life cycle (Fayt et al. 2006). As already discussed, such gaps caused by windthrow or the collapse of overmature trees were present even before modern forestry started to alter the forests of the study area. These sites provide warmer microclimates, which are especially preferred where temperature is a factor limiting the survival of populations (Warren and Key 1991), as in the montane zone of the National Park "Bavarian Forest". Meadows adjacent to forests have a richness and diversity of Aculeata and Heteroptera similar to that of gaps. This can be explained by the inflorescences and a high diversity of plant species, which are provided by both types of openings but not by closed forests. Moreover, differences in leaf chemistry and architecture of shrubs and tree saplings compared to mature trees may play a role for sap-sucking insects (aphids, true bugs) (Schowalter 1985). This is also supported by the increase of Aculeata species during the first several years on a spruce windthrow gap in an alpine forest (Duelli et al. 2002b; Wermelinger et al. 1995). Our species indicator analysis found different species characteristic for meadows and gaps in all three taxonomic groups. In meadows a greater number of ubiquitous species was found (Table 1), especially among the true bugs. In gaps most of the recorded species were inhabitants of complex habitats and occurred only where inflorescences, trees and dead wood are available together. Even if richness patterns of gaps and meadows are similar, a higher species density of saproxylic beetles, including the threatened species, was found only in gaps. Therefore we can conclude that the quantitative species density in meadows and gaps is dissimilar, and that the latter support a larger number of species characteristic for forest conditions and specialists requiring complex forest habitats. This underscores the importance of *Ips typographus* as a habitat engineer within forests.

Canopy as alternative habitat to edges/openings

The number of species found in the tree crowns was relatively low. This agrees with studies on several taxonomic groups in Central European forests (Bächli et al. 2006; Hacker and Müller 2007; Wermelinger et al. 2007). In contrast, species of some groups such as jewel beetles, several true bugs and the lace wings are often more abundant in the canopy (Floren and Schmidl 1999; Gruppe et al. 2007; Gruppe and Müller 2006; Schubert and Gruppe 1999; Wermelinger et al. 2007), but with the exception of true bugs these were poorly represented in our study (Müller et al. 2007a). Trees with green branches down to ground level, a normal condition for edge trees, offer an opportunity to trap or collect even typical arboricolous canopy species such as true bugs and some saproxylic beetles close to the forest floor (Gruppe et al. 2007; Stork et al. 2001). The apparently low number of species with a preference for the canopy in our study was influenced by this descent of normally canopy-dwelling species at the edges. It must be concluded, however, that in temperate forests the availability of dead wood, young trees and herbaceous species near the ground results in general in a more diverse habitat for insects than that provided by tree crowns.

Ips typographus as a keystone species

The definition of keystone species is primarily based on the observation that in many ecosystems certain species have an unusually high number of relationships with other organisms in their community (Simberloff 1998). The definition has been expanded (Menge et al. 1994), so that species may also qualify as keystones by virtue of how they change the environment, e.g. beavers *Castor canadensis* because of their dams (Naiman et al. 1986), gopher tortoises through their burrows which form a home for other species (Jackson and Milstrey 1989) or European bee-eater *Merops apiaster* which provides food and places to nest and roost for many other species in arid areas (Casas-Crivillé and Valera 2005). Christianou and Ebenmann (2005) defined three types of keystone species based on theoretical models of extinction. Using this classification *I. typographus* can be identified as the abundant intermediate species type, interacting strongly with many resources. A high keystone index (Jordán et al. 2006) can also be attributed to *I. typographus* not only because of the high number of species directly interacting with it (Weslien 1992), but also as shown by our study because of the numerous other forest insects which benefit from bark beetle gaps. However, this definition of keystone species can be further restricted by the consideration of low redundancy as a criterion (Kotliar 2000). If this bark beetle could be excluded, windthrow would produce similar openings in the study area, as shown to have existed in past centuries even under old-growth conditions and in the 1980s also in former commercial stands. A direct comparison between windthrow areas and beetle gaps was not possible in this study, because recent windthrow gaps were not available. But we have to keep in mind that bark beetles produce a structure which nevertheless shows some clear differences to windthrow gaps; with more snags than lying trees, and no root plates. The reality in Central European montane forest is that windthrow and *I. typographus* occurrence are strongly linked in forests containing spruce, and can probably only theoretically be separated in the landscape. However, we can conclude that within the area of the National Park, by driving a process resulting in greater diversity of insect taxa in formerly commercial, dense forests, the former pest species undoubtedly fulfils the majority of criteria for a keystone species.

Management implications

The keystone concept is a useful tool for communicating the importance of ecology to the public (DeMaynadier and Hunter 1994), especially in species with bad public reputations, such as the most feared bark beetle species in Central European forestry. The study of uncontrolled disturbance regimes teaches us much about insect "calamities" in montane forests. It is important to stress that in the montane zone most insects seem not to be edge species as indicated by Duelli (2006), but gap species as shown in our study. Coming back to the question of the ecological justification for "wilding" (non-interference with natural processes), we conclude that insect disturbance on the landscape scale is an important factor in the maintenance of biodiversity. It results in more complex habitat conditions, which benefit other insects. In the area of the National Park "Bavarian Forest" the infestation by bark beetle has created sunny openings and caused an increase in dead wood availability. In relict old-growth stands with a relict saproxylic fauna, an attack also increases availability of dead wood (Müller et al. 2005a). This is a first step on the way back to an increased structural diversity of the forest landscape and could save from extinction some of the saproxylic species which still survive as "living dead" in isolated refuges (Müller et al. 2007a).

Whilst not denying these important ecosystem services, we have to observe that Norway spruce plantations are widely distributed today even at lower altitudes, where conditions are much more favourable for *I. typographus* than in montane forests. As a consequence of this, but exacerbated by climate warming, we have to expect a further increase of spruce tree infestation by bark beetles in the near future (Jönsson et al. 2007). This is not likely to be viewed positively by the forest industry, because of serious economic penalties. From an ecological point of view, a large scale infestation where spruce is the only tree species could negatively influence other forest species (Koprowski et al. 2005; Scherzinger 2007). On the other hand, studies on soil fauna in the montane spruce forest have shown that logging of infested spruce stands at high elevations results in the extinction of rare Collembola, while release of bark beetle areas by non-interference sustained this soil fauna (Rusek, pers. commun.). In conclusion, we derive from our study the following recommendations for conservation in montane, forested areas of Central Europe:

1. Bark beetle infestations in montane forests have been typical for this habitat even before modern forestry began, and many insect species benefit greatly from the increase of habitat diversity and temperature found in bark beetle gaps.
2. For economic reasons, uncontrolled infestations will be restricted to protected areas. However, the creation wherever possible of similar gaps, even in logged forests, would benefit forest-dwelling insects in general.
3. To simulate this type of natural disturbance, logging in medium-aged mixed montane stands should aim to create gaps with retention of a part of the dead wood. Planting after logging should be delayed, to lengthen this important phase of sunlit conditions otherwise rarely found in a landscape of young and dense commercial forests.

Finally, the application of the keystone species concept to *I. typographus* improves our understanding of the effects of natural disturbance on biodiversity, beyond the prevailing, purely economic views on this serious pest.

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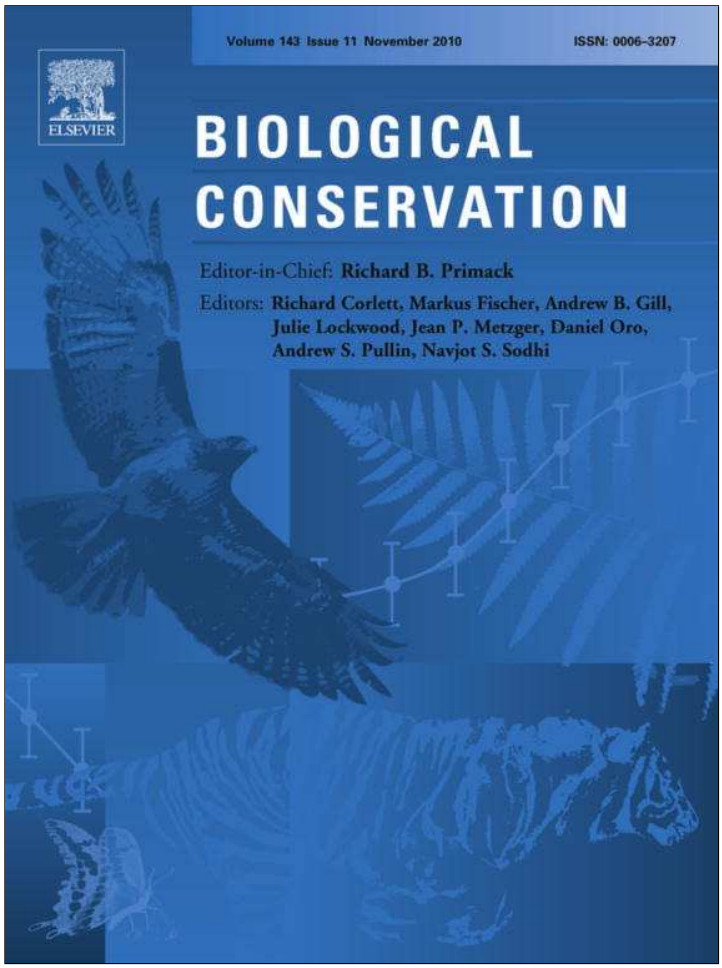
Artikel II



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Learning from a "benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation

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ABSTRACT

Increasing demands for firewood owing to rising energy costs have accelerated discussions about the amount of dead wood needed for conservation. A sharp increase in dead wood caused by bark beetles in a German national park provides lessons for management of commercial and protected forests. We investigated the effects of dead wood due to bark beetle infestation as well as tree senility on abundance and richness of saproxylic species of beetles. Increasing amounts of spruce dead wood and opening of the canopy by bark beetles had positive effects on the abundance of host-generalist, conifer-specialist, and red-listed saproxylic beetles. Broadleaf specialists were positively associated with the amount of broadleaf dead wood and negatively associated with canopy openness. Gradient analysis of beetle assemblages revealed two major environmental axes: canopy openness and amount of dead wood. We found a threshold for community divergence at a canopy openness of 23% (confidence interval CI: 11–49) and at an amount of dead wood of 64 m^3 ha^{-1} (CI: 35–160). Critically endangered species served as indicators of dense and open forests, but only when the amount of dead wood was high. Our results suggest that, to maintain saproxylic beetle assemblages, the amount of dead wood in commercial montane forests (at present ≈15 m^3 ha^{-1}) needs to be tripled, with a focus on broadleaf wood in dense stands and spruce wood in open stands. For large protected areas in Europe, our data suggest that bark beetle infestation and senescence without active forest management improves habitat conditions for saproxylic beetles.

1. Introduction

Approximately 25% of all species in European forests (mainly fungi and beetles) are involved in the decomposition of dead wood (Jonsson et al., 2005). Human activities have reduced the amount of dead wood in managed forests considerably, such that many species associated with dead wood appear on Red Lists (Grove, 2002). To support viable populations of saproxylic species, forest authorities are considering various strategies for increasing dead wood in managed forests (Davies et al., 2008; Wikberg et al., 2009). Recently, however, rising energy costs have increased the price of firewood. This economic pressure has refreshed discussions about the amount of dead wood in managed forests (Jonsell, 2007).

Saproxylic beetles are defined as those that depend on dying and/or dead wood as well as on wood-inhabiting fungi during some part of their life cycle (Speight, 1989). They play important roles in the ecosystem as decomposers, predators, or vectors for fungi (Paine et al., 1997). Only a minority of saproxylic species are able to kill living trees (i.e., 34 of the 122 scolytids on trees in Central Europe; Grodzki et al., 2006; Lieutier et al., 2004; Parker et al., 2006). In forests with no economic constraints on management, these "pest" species can play a positive role as ecosystem engineers (Jones et al., 1994) by controlling the availability of resources to other species (Buse et al., 2008).

Over the last 20 years, bark beetle outbreaks occurred in the USA (mountain pine beetle; Raffa et al., 2008) and Central Europe (European spruce bark beetle; Schelhaas et al., 2003), (Baláž, 2009; Grodzki, 1998; Jonášová and Pracha, 2004; McFarlane et al., 2006). Furthermore, a spread of such outbreaks to the boreal and alpine zones is predicted by models incorporating global warming (Jönsson et al., 2009; Williams and Liebhold, 2002). Therefore, the ecological and economical importance of such large-scale disturbances in forests might become even larger in the future (Schroeder, 2007). Up to now, however, discussion about the "engineering" role of bark beetles has focused mainly on responses of mammals and birds (Koprowski et al., 2005; Martin et al., 2006).

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Insect outbreaks are one of several sources of disturbance in forests (Schelhaas et al., 2003). Like fire and windstorm events, insect outbreaks create substantial amounts of dead wood and open the canopy across large areas (Schroeder, 2007). The majority of studies investigating saproxylic beetles have concentrated on logging practices or small-scale disturbance, such as senescence of single trees or crown damage by windstorms in old-growth stands; only a few studies have investigated the impact of medium- to large-scale natural disturbances on saproxylic beetles (Table S1/S2). The latter are biased toward fire and wind (Bouget and Duelli, 2004; Grimbacher and Stork, 2009). To the best of our knowledge, only one study to date has investigated the effect of bark beetle disturbance on the diversity of saproxylic beetles (Müller et al., 2008a).

In Central Europe, the Bavarian Forest National Park was the first protected forest affected on a large scale by bark beetles. Therefore, this park serves as a pilot study area for Central Europe, from which management guidelines can be developed for commercial forests and strictly protected areas with a "benign neglect" strategy (Zahner, 1992). Such a strategy is not always appreciated aesthetically by the public (Lindenmayer et al., 2004; Müller and Job, 2009; Stokstad, 2006). The objectives of our study are twofold:

1. To analyze the relationship between features of natural dynamics and the abundance, species richness, and community composition of saproxylic beetles of different levels of host specialization.
2. To determine the minimum amount of dead wood needed for the conservation of comprehensive saproxylic beetle assemblages and the minimum level of canopy openness needed for species of open areas.

2. Methods

2.1. Study area and study sites

To assess the effects of dead wood accumulation and canopy opening by bark beetle infestations and single-tree senility on saproxylic beetles, we established sampling plots within 24,000 ha of the Bavarian Forest National Park, founded in 1970 in the southeastern corner of Germany (for a map, see Müller and Brandl, 2009). The cool, temperate, montane forests of the park are dominated by spruce (*Picea abies*) at 1150–1430 m, and at lower elevations above 650 m by mixed stands of spruce, beech (*Fagus sylvatica*), and fir (*Abies alba*). The climate and acidic soils are rather homogenous (Bässler et al., 2008). Although trees were logged in these mountains to produce charcoal for glass production and to create pastures, human influence was low up to the mid 19th century. At that time, after large windstorms and subsequent damage by bark beetles, modern forestry began and changed tree species composition. Before long, old-growth stands remained only as small patches of ca. 100 ha. Coupled with these changes, some beetle species associated with old forests (i.e., *Peltis grossa* and *Lacon lepidopterus*) became extinct. Today, we can divide the park area into three categories of forest management:

1. *Old-growth relict* forests are interspersed small stands dominated by veteran trees >400 years old, which have not been logged for >50 years; in these stands, dead wood of Silver Fir and European Beech increased during these 50 years because of senility, crown damage, and single tree falls; but also spruce trees were killed by bark beetles.
2. *Unmanaged* forests in the southern part of the national park are dominated by spruce, which have died back mainly because of infestation by bark beetles (*Ips typographus*) across large areas. This process started in the early 1990s (Müller et al., 2008a).
3. *Managed* forests in the northern part of the national park and in the buffer zone around the park are subject to intensive salvage logging of all bark-beetle-infested spruce trees.

We established 293 plots of 0.1 ha, each along four transects (total length = 29.3 km) spanning the altitudinal gradient, plus an additional 500-m transect in an old-growth stand at higher altitude to obtain data on a beech-fir old-growth stand at higher elevation. We sampled beetles from 126 randomly selected plots with a minimum distance of 100 m (21 in old-growth relicts, 52 in unmanaged areas, 53 in managed areas; Bässler et al., 2008; Müller and Brandl, 2009).

2.2. Beetle data

Logistical constraints dictate the methods of beetle sampling, particularly in remote areas. We followed the suggestion of Martikainen and Kouki (2003) for sampling saproxylic beetles in boreal forests by combining various methods (Fig. S1). We used three different methods at each plot: (1) in the center of each plot, we installed one flight-interception trap consisting of a crossed pair of transparent plastic shields (40×60 cm); (2) to sample species that are flightless for most of their life cycle (e.g., genus *Acalles*), we installed one pitfall trap under each flight-interception trap (for more details, see Müller and Brandl, 2009), and (3) to avoid a bias of capturing only active individuals, an experienced entomologist (H. Bussler) searched appropriate substrates in each 0.1-ha plot for 45 min in July 2007 over a period of 3 weeks, under sunny and warm weather conditions.

All the sampled beetles were identified to the species level (Freude et al., 1964–1983) and classified as saproxylic or non-saproxylic according to Schmidl and Bußler (2004). Because the bark beetle *I. typographus* is the main agent for providing spruce dead wood, we excluded this species from our analyses. We grouped all saproxylic species according to their host species during larval development into the following guilds (Gibb et al., 2006): (1) specialists on broadleaf trees, (2) specialists on coniferous trees, and (3) generalists living on dead wood of broadleaf and coniferous trees (Koch, 1989–1992; Köhler, 2000). In addition, we quantified the number of red-listed species, summarizing the species of the IUCN classifications from vulnerable to regionally extinct using the most up-to-date Red List for Bavaria (Schmidl et al., 2003). Remaining species were classified as others. For each group, we totaled the number of individuals as a surrogate of abundance and the number of species per sampling plot. After visual inspection, the abundance estimates, the number of species of broadleaf and conifer specialists and the number of red-listed species were $\log_{10}(x+1)$ transformed to approach a normal distribution. Use of a linear model for all dependent variables enabled us to compare the explanatory power of all models using R^2. We used the presence/absence data of species, including only species with an occurrence of at least three plots, for indirect gradient analyses.

2.3. Environmental variables

We restricted our environmental sampling to 0.1-ha plots, which are sufficiently large to avoid unrealistic high estimates but small enough to capture small-scale variation (Müller et al., 2008b; Økland et al., 1996). From a comprehensive set of environmental variables (Bässler et al., 2008), we selected four variables that characterize forest dynamics caused by bark beetle infestation and single-tree senility. We calculated the amount of dead wood ($m^3\ ha^{-1}$) on an area of 1 ha of (1) Silver Fir, (2) Norway Spruce, and (3) broadleaf trees (consisting almost entirely of European Beech, with <1% of Mountain Ash and maple). We included all pieces of wood with a diameter $\geqslant 0.12$ m (the standard minimum

in dead wood inventories in Central Europe) by up-scaling from 0.1 ha in a circle around the traps. Volume equations of the standing dead trees are based on tree species and diameter at breast height; the volume of logs and snags was calculated assuming a cylinder and using the length and diameter at half length (Bässler et al., 2008). We considered Silver Fir and Norway Spruce separately because fir is host to some typical coniferous beetle species as well as to some species that inhabit broadleaf trees. After visual inspection of the distribution of our data, we $\log_{10}(x+1)$ transformed the amount of dead wood per plot, which resulted in an almost normal distribution for further analyses. A square-root transformation produced almost identical results. Following Siitonen et al. (2000), we additionally calculated the diversity of dead wood (Fig. S3). (4) Canopy openness was measured by airborne laser scanning using the penetration rate of LiDAR impulses at 2 m above ground (Müller and Brandl, 2009). Across our plots, the penetration rate decreased with increasing bark beetle attack. More-open stands may be important for many saproxylic organisms in montane areas because these stands provide warm and dry habitats, as well as flowers (Bouget and Duelli, 2004).

To control for effects independent of the forest dynamics in our montane area, we used elevation (Körner, 2007) and the binary variable habitat continuity (Jonsson et al., 2005) as covariates; the 21 plots in old-growth relicts were scored as plots with long habitat continuity. Habitat continuity is difficult to quantify (Sverdrup-Thygeson, 2001), but could be important because some species of saproxylic beetles depend on a continuous availability of old decaying trees (Jonsson et al., 2005; Speight, 1989).

2.4. Statistical analyses

We analyzed the relationship of beetle abundance and species richness to habitat factors using multiple regressions. To check the residuals of our models for spatial independence (Dormann et al., 2007), we used cross-correlograms provided by the add-on package *ncf* (Bjørnstad and Falck, 2001) in R (R Development Core Team, 2008). The residuals of our models showed no spatial autocorrelation even at very small distances (Fig. S2); therefore, we ignored space in subsequent analyses. To separate the effects of abundance (individuals of beetles) and species richness, we first concentrated our analysis on the number of individuals of each group; for the analysis of species richness, we used the $\log_{10}$ number of individuals as a covariate (Gotelli and Colwell, 2001).

The amount of dead wood in our plots was highly correlated with the diversity of dead wood ($r^2 > 0.7$; Fig. S3). This fact constrains any attempt to separate the two factors in observational studies. Therefore, we concentrated in further analyses on the amount of dead wood because it is easier to measure and to communicate to foresters and conservationists. For generalists, which can feed on both conifers and broadleaf trees, we used the total amount of dead wood as the predictor; for specialists, both common and red-listed species, we used the amount of dead wood separated in our three tree species groups. Elevation and habitat continuity were included as covariates in all models. We detected no interactions between predictors.

To compare the explanatory power of large-scale disturbance by bark beetles, with that of small-scale effects due to tree senility, we built three predictor sets of environmental variables (*Bark beetle*: dead wood of spruce, penetration rate; *Senility*: dead wood of fir and beech; *Control*: elevation and habitat continuity). We partitioned the variation of responses with respect to the three explanatory variable sets using the function *varpart* in vegan (Oksanen et al., 2006). This application uses partial multiple regression analysis. We calculated adjusted R^2 values because this is the only unbiased method (Peres-Neto and Jackson, 2001). The community was analyzed with a partial canonical correspondence analysis, which does not provide adjusted R^2. To test the significance of the influence of our independent fractions on beetle data, we applied a permutation test with 1000 permutations using the function *anova* in *varpart*. To determine the errors of our independent fractions, we used 1000 bootstrapping samples, which allowed the construction of 95% confidence intervals.

To display variation in species composition among the study plots, we used unconstrained correspondence analysis (CA). Furthermore, we used the function *adonis* (analysis of variance between groups of assemblages) in *vegan* with Bray-Curtis dissimilarity to test for significant differences in species composition between the three management types (managed, unmanaged, old-growth relict) with a Bonferoni correction for multiple testing (Anderson, 2001). To identify community shifts along a gradient of increasing dead wood amount and penetration rate (Andersen et al., 2009), we applied a conditional inference tree using the function *ctree* in the package *party* (Hothorn et al., 2006) with total amount of dead wood or penetration rate as predictor and site scores of correspondence analysis as dependent variable. This tree method is robust for all types of distribution of the independent and dependent variables (Hothorn et al., 2006). A confidence interval for the threshold was calculated using 1000 bootstraps (Roff, 2006). For testing of nestedness in our community, we used the function *nestedtemp* (Rodríguez-Gironés and Santamaria, 2006) in *vegan*. To identify species with a preference for low or high amounts of dead wood, and dense and open canopy stands identified by conditional inference trees, we applied indicator species analysis for species ($p < 0.05$) with a minimum occurrence in three plots and considered their abundance (Dufrêne and Legendre, 1997).

3. Results

Among managed forests, unmanaged forests, and old-growth relicts, we found clear differences in the amount and composition of dead wood (Fig. 1). The highest amount of dead wood, dominated by spruce and caused by bark beetle infestation, was found in unmanaged areas (Fig. 2, Table S3). The amount of dead wood in portions of the national park subjected to salvage logging was about one order of magnitude lower than in unmanaged areas

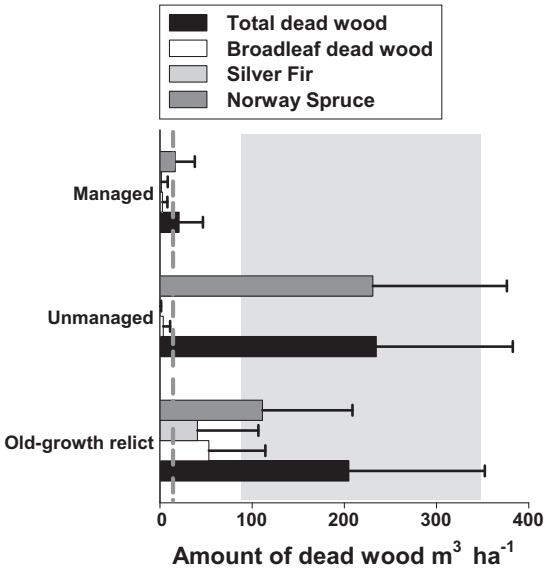

Fig. 1. The amount of dead wood (mean and standard deviation) of the various tree species in the three management-type areas within the Bavarian Forest National Park. The shaded box shows the range of dead wood in mixed montane Norway Spruce–Silver Fir–European Beech forests in Europe (Christensen et al., 2005).

Fig. 2. The amount of dead wood in the Bavarian Forest National Park caused by natural dynamics of large-scale bark beetle disturbance and small-scale tree senility varies greatly from 5 m^3 ha^{-1} to 700 m^3 ha^{-1}.

and was similar to that found in the adjacent, commercial forests (14 m^3 ha^{-1}; dashed line in Fig. 1).

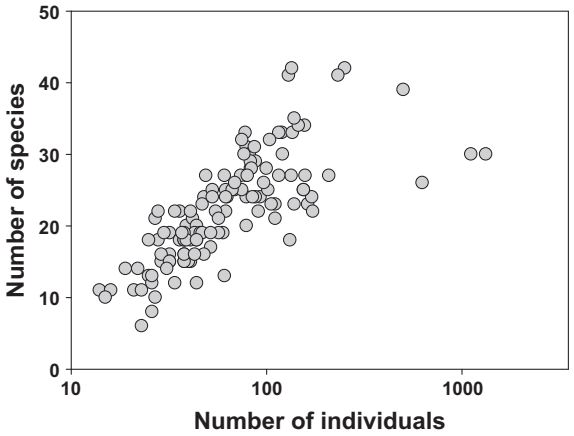

Fig. 3. Correlation of individuals and species of saproxylic beetles sampled with direct search, flight-interception traps, and pitfall traps at 126 sites. *Ips typgrographus*, the main agent of spruce dead wood, is excluded.

After excluding the bark beetle *I. typographus*, our final data set comprised 12,257 individuals of saproxylic beetle species belonging to 280 species. Flight-interception traps yielded 244 species (103 exclusive), pitfall traps 33 species (1 exclusive), and direct searching 164 species (22 exclusive). Seventy-eight species were red-listed species. Most saproxylic beetle species (113) were generalists, as judged by their larval hosts; 90 species inhabited dead wood of coniferous trees, and 77 species inhabited dead wood of broadleaf trees. The number of species was clearly correlated with the number of individuals (Fig. 3).

The variance partitioning with three predictor sets (*bark beetle*, *senility*, *control*) revealed that bark beetle had the highest independent effect on the abundance of generalists, conifer specialists, and red-listed species (Fig. 4). The abundance of common species and broad-leaved specialists was more affected by single-tree senility of broad-leaved and fir trees. Our linear models with abundance as a dependent variable showed that amount of dead spruce had a positive effect on red-listed species. The amount of dead wood of broadleaf trees had a positive influence on the abundance of broadleaf specialists, red-listed species, and common species; the total amount of dead wood had a positive effect on the abundance of generalists (Table 1). Conifer specialists were positively affected only by increasing penetration rate, which was important for almost all dependent variables. Broadleaf specialists were the only group negatively affected by increasing penetration rate. The multiple R^2 showed that the model for red-listed species had the highest explanatory power, which decreased to the model for other species (Table 1). After taking into account the $\log_{10}$(number of individuals), the species richness of generalists was significantly and positively influenced by the total amount of dead wood. Species richness of conifer specialists increased, whereas species richness of red-listed species decreased with increasing penetration rate (Table 1).

For community composition, the independent effects of the variance partitioning were similar for the data sets capturing the effects of bark beetle, senility, and elevation (control). The analysis of the composition of beetle assemblages using unconstrained correspondence analysis supported the above findings. The first ordination axis extracted by correspondence analysis was correlated to the penetration rate (Fig. 5; $r^2 = 0.83$) and elevation (Fig. 5; $r^2 = 0.76$), whereas the second axis represented a gradient of the amount of dead wood (from low to high resource availability; Fig. 5; $r^2 = 0.65$). Therefore, the second axis mirrors the increase in the amount of dead wood in unmanaged areas on the composition of beetle communities. A constrained canonical

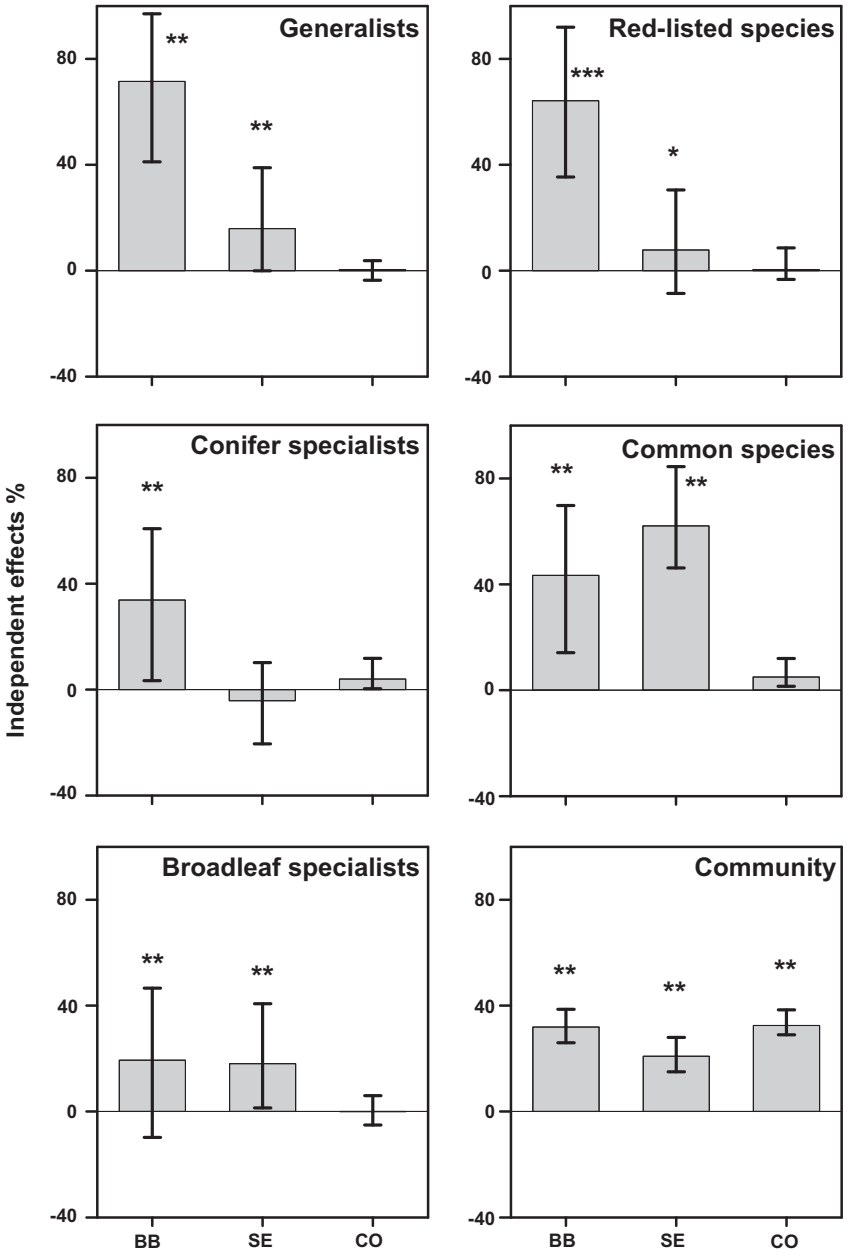

Fig. 4. Exclusive explanatory contribution of bark beetle infestation (BB), single-tree senility of broadleaf and Silver Fir (SE), and control variable sets (CO) with elevation and habitat continuity, of the total explained variance for each dataset based on variance partitioning, using the function varpart in vegan (Oksanen et al., 2006) for the abundance and a canonical correspondence analysis application for community. To test the significant influence of each independent fraction on the independent variables, a permutation test was applied using the function *anova* in vegan; significant p-values are indicated by asterisks: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. To display the variability of our independent fractions, a bootstrapping of variance partitioning was additionally applied, and the 95% confidence interval is shown in the box plots by whiskers. Note that the significance by permutation and the confidence intervals shown by the whiskers are not related to each other. Also note that the target variables differ significantly from each other (vector, community matrix); they cannot be compared quantitatively among each other.

correspondence analysis using penetration rate as the single predictor revealed a constrained inertia of 0.29 (expected inertia assuming random distribution of species; 95% CI: 0.04–0.07). The total amount of dead wood as single predictor led to a constrained inertia of 0.16. This was again significantly larger than expected from a random distribution (95% CI: 0.04–0.07). Bootstrapping with 1000 replicates revealed that the constrained inertia of the penetration rate was significantly ($p < 0.001$) larger than the value for dead wood.

The unmanaged plots followed the direction of increasing amount of dead wood along the second axis, similar to the old-growth relicts. However, the community composition of these two forest categories rich in dead wood were distinct (*adonis* post hoc difference, $p < 0.01$). A simulation test of the reliability of the ordination axis and its correlation with penetration rate and the total amount of dead wood showed two important results (Fig. S4). First, the comparatively low proportion of variance summarized by the first two axes of the CA is a result of the large number of community samples. Secondly, when more than 70 communities were sampled, the penetration rate was always significantly correlated with axis 1 and the amount of total dead wood was correlated with axis 2. The application of an NMDS or a direct

Table 1
Models estimated by multiple linear regressions 1 for saproxylic beetles grouped according to substratum host specification and level of endangerment (for classifications, see Section 2). Estimates are based on mean-zero unit variance standardized independent variables; na = not analyzed.

Dependent variable	R^2	Individuals	Elevation	Habitat continuity	Spruce	Broadleaf	Fir	Total dead wood	Penetration rate
Abundance									
Generalists	0.37	na	−0.10	0.15*	na	na	na	0.36***	0.30***
Broadleaf specialists	0.34	na	−0.12	0.00	−0.04	0.41	−0.08	na	−0.40
Conifer specialists	0.27	na	0.05	−0.21	−0.05	0.01	−0.02	na	0.52***
Red-listed species	0.43	na	0.02	0.14	0.28***	0.24***	0.09	na	0.43***
Other species	0.17	na	−0.01	−0.15	0.02	0.34***	0.07	na	0.29**
Species									
Generalists	0.61	2.38***	−0.92***	0.05	na	na	na	1.08***	0.16
Broadleaf specialists	0.88	0.71***	−0.08*	0.01	−0.01	−0.01	−0.00	na	−0.01
Conifer specialists	0.76	0.44***	−0.01	−0.00	−0.01	−0.03	−0.02	na	0.11*
Red-listed species	0.71	0.51***	0.02	0.04	0.02	−0.04	0.02	na	−0.10*
Other species	0.49	4.67***	−1.42	−0.48	0.35	0.10	−0.66	na	0.82

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

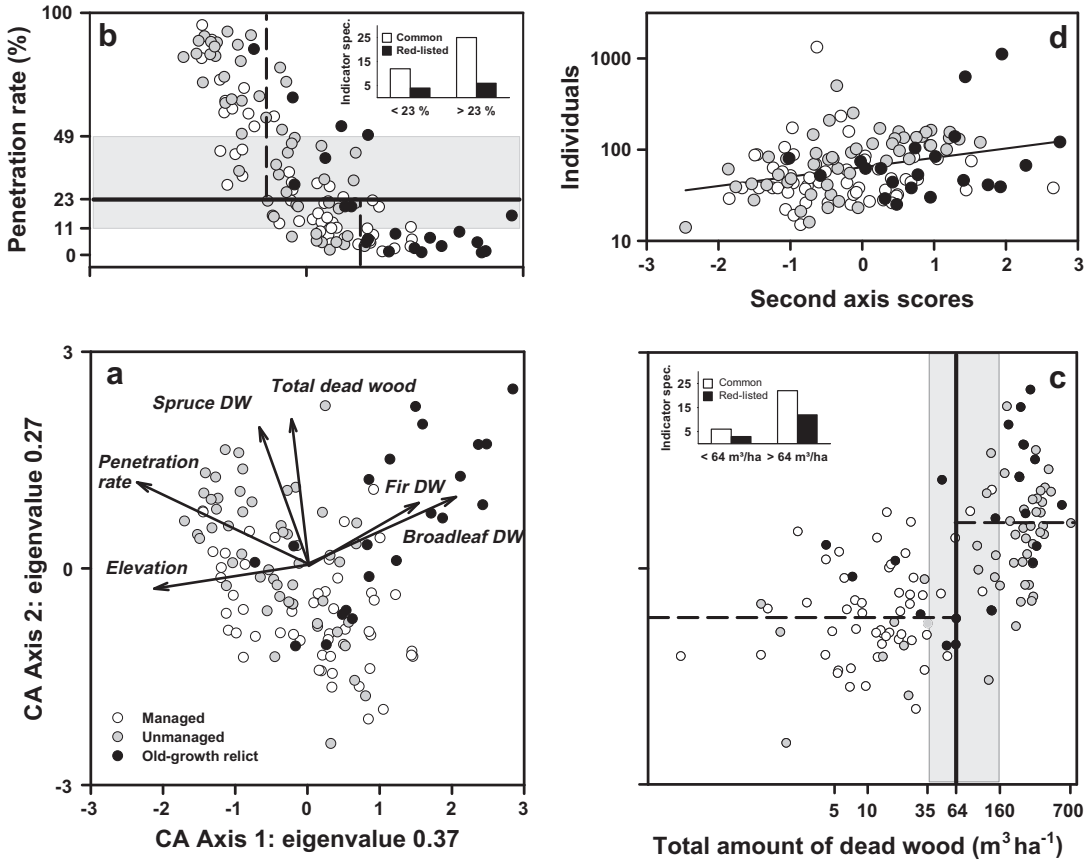

Fig. 5. Unconstrained correspondence analysis of presence/absence data of 126 saproxylic beetle samplings with species occurring in at least three plots. The percentage of explained variance is 5% for axis 1 and 3.3% for axis 2. The environmental variables were fitted on the plot using *envfit* in vegan. (a) Scores of each site in the three different types of management areas. (b) Scatterplot showing the site scores of the first correspondence analysis axis versus penetration rate. The horizontal line indicates the threshold value for the maximum difference in community with a 95% confidence interval (gray shading); the bar plot at the top shows the number of species with a significant indicator value for dense and open forests. (c) Scatterplot showing the site scores of the second correspondence analysis axis versus dead wood amount. The vertical and the gray area again shows the threshold with the 95% confidence interval; the bar plot at the top shows the number of indicator species. (d) Scatterplot of the scores of the second axis plotted against the number of individuals.

ordination using canonical correspondence analysis supported our interpretation of the first two ordination axes (Fig. S5/S6). Taking both results into account, we conclude that our results are robust. Note also that our results are not due to differences in abundance between plots, because the analysis was restricted to the presence/absence of species.

When we applied the conditional inference tree to the correspondence analysis scores (Fig. 5) of the first axis with penetration rate as predictor, a split (=threshold) with a non-linear shift (Fig. 5b) of community occurred at 23% penetration rate (95% CI: 11–49%). The conditional inference tree of the site scores of the second axis revealed a split at 64 m^3 ha^{-1} of dead wood (95% CI:

Table 2
Preference of single species [taxonomy according to Köhler and Klausnitzer (1998)] for dense and open canopies (threshold 23% canopy openness = CO), and for low and high amount of dead wood (threshold 64 m^3 ha^{-1} dead wood = DW) stands, using indicator species analysis (IV = indicator value) (Dufrêne and Legendre, 1997). Conservation status according to the Red List of Bavaria (Schmidl et al., 2003): VU = vulnerable, EN = endangered, CR = critically endangered; substratum according to Schmidl and Bußler (2004): fresh = fresh dead wood, decomposed = decomposed dead wood, fungi = wood-inhabiting fungi.

Species	Host speciation	Substratum	Red List	IV DW	*p* DW	IV CO	*p* CO
	Dense forest with low volume of dead wood						
Salpingus ruficollis	Broadleaf	Fresh		41.2	<0.001	47.3	<0.001
Xyloterus domesticus	Broadleaf	Fresh		38.8	<0.001	39.5	<0.001
Xyleborus dispar	Broadleaf	Fresh		16.4	0.022	18.3	0.007
	Dense forest with high volume of dead wood						
Bolitophagus reticulatus	Broadleaf	Fungi	VU	20.3	0.005	16.3	0.043
Ceruchus chrysomelinus	Generalist	Decomposed	EN	11.1	0.040	15.4	0.005
	Dense forest						
Cychramus variegatus	Generalist	Fungi				50.4	<0.001
Melanotus castanipes	Generalist	Decomposed				47	0.026
Ernoporicus fagi	Broadleaf	Fresh				27.9	0.021
Quedius xanthopus	Generalist	Decomposed				27.1	<0.001
Micrambe abietis	Conifers	Fungi				22.5	0.022
Quedius plagiatus	Generalist	Decomposed	VU			21.3	0.003
Acalles camelus	Broadleaf	Decomposed				17.1	0.004
Atrecus pilicornis	Conifers	Decomposed	VU			15.9	0.012
Hedobia imperialis	Broadleaf	Decomposed				14.6	0.007
Acalles hypocrita	Broadleaf	Decomposed				14.1	0.002
Cis glabratus	Generalist	Fungi				11.9	0.021
	Open forest with low volume dead wood						
Ernobius abietis	Conifers	Decomposed		20.8	0.0114	19.5	0.03
	Open forest with high volume dead wood						
Anaspis rufilabris	Generalist	Decomposed		57.5	0.017	82.5	<0.001
Ampedus auripes	Conifers	Decomposed	VU	28.2	0.0066	51.6	<0.001
Ampedus nigrinus	Generalist	Decomposed		46.3	<0.001	50.7	<0.001
Pityophthorus pityographus	Conifers	Fresh		52.9	<0.001	47.8	<0.001
Dasytes niger	Generalist	Decomposed		28.9	0.0024	44.8	<0.001
Ampedus aethiops	Conifers	Decomposed		28.8	0.0012	42.8	<0.001
Oxymirus cursor	Generalist	Decomposed		26.1	0.0326	40.5	<0.001
Judolia sexmaculata	Conifers	Decomposed	EN	21.3	0.0032	32.3	<0.001
Pteryngium crenatum	Generalist	Fungi	VU	39.4	0.0002	28.0	0.002
Corymbia rubra	Conifers	Decomposed		21	0.0058	26.6	<0.001
Thymalus limbatus	Generalist	Fungi	VU	25.4	<0.001	26.5	<0.001
Dictyopterus aurora	Generalist	Decomposed		24.6	0.0066	24.6	0.005
Crypturgus cinereus	Conifers	Fresh		28.6	<0.001	22.9	0.008
Diacanthous undulatus	Generalist	Decomposed	VU	17.8	0.001	19.4	<0.001
Crypturgus pusillus	Conifers	Fresh		13.1	0.0268	14.4	0.01
Tachyta nana	Generalist	Decomposed		11.7	0.0046	11.3	0.005
Hadreule elongatulum	Conifers	Fungi	VU	8.3	0.0216	8.1	0.026
	Open forest						
Rhagium bifasciatum	Generalist	Decomposed				47	0.04
Hylastes cunicularius	Conifers	Fresh				42.4	0.012
Dryocoetes autographus	Conifers	Fresh				37.4	0.007
Polygraphus poligraphus	Conifers	Fresh				33.1	0.004
Rhizophagus ferrugineus	Conifers	Fresh				28.3	<0.001
Dasytes obscurus	Conifers	Decomposed				26.1	<0.001
Rhyncolus ater	Generalist	Decomposed				26	0.034
Stenurella melanura	Generalist	Decomposed				25.2	<0.001
Rhizophagus dispar	Generalist	Fresh				23	0.035
Leptusa fumida	Generalist	Decomposed				14.5	0.001
Nudobius lentus	Generalist	Fresh				11.3	0.008
Anostirus castaneus	Generalist	Decomposed				9.7	0.013
Hylurgops palliatus	Conifers	Fresh				9.7	0.011
	Low volume of dead wood						
Corticarina lambiana	Conifers	Fungi		34.4	0.006		
Corticaria abietorum	Conifers	Fungi	VU	26	0.041		
Xylechinus pilosus	Conifers	Fresh		19.7	<0.001		
Tetratoma ancora	Broadleaf	Fungi	VU	15.9	0.003		
Triplax russica	Broadleaf	Fungi	VU	15	0.021		
	High volume of dead wood						
Ampedus erythrogonus	Generalist	Decomposed	VU	25.4	0.006		
Gyrophaena boleti	Generalist	Fungi		24.7	0.002		
Ostoma ferruginea	Generalist	Fungi	VU	21.2	0.008		
Rhagium mordax	Generalist	Fresh		18.9	0.038		
Atrecus affinis	Generalist	Decomposed		18.5	0.002		
Anisotoma humeralis	Generalist	Fungi		15	0.013		
Ipidia binotata	Generalist	Decomposed	CR	15	<0.001		
Dorcatoma punctulata	Generalist	Fungi	EN	13.3	0.003		

(*continued on next page*)

Table 2 (*continued*)

Species	Host speciation	Substratum	Red List	IV DW	*p* DW	IV CO	*p* CO
Latridius consimilis	Broadleaf	Fungi	CR	11.7	0.005		
Anastrangalia dubia	Conifers	Decomposed		10	0.01		
Anisotoma castanea	Generalist	Fungi		8.3	0.021		
Bolitochara mulsanti	Generalist	Fungi		8.3	0.024		
Cerylon histeroides	Generalist	Decomposed		8.3	0.021		
Hexarthrum duplicatum	Generalist	Decomposed	CR	8.3	0.023		
Corticeus linearis	Conifers	Fresh		6.7	0.047		
Xestobium austriacum	Conifers	Decomposed	EN	6.7	0.046		

35–160 m^3 ha^{-1}; Fig. 5c; see also Fig. S6). Nevertheless, the scores of the second axis were slightly correlated with the number of individuals but clearly correlated to the number of species ($r^2 = 0.35$, $p < 0.001$) (Fig. 5d). Our test for nestedness revealed a significant ($p < 0.001$) nestedness temperature of 23.6.

The species indicator analysis revealed 16 species with a significant indicator value for stands with a penetration rate <23%, three of which were also indicators for low amount of dead wood (<64 m^3 ha^{-1}) and two for high amount of dead wood (Table 2). The analysis revealed 31 species with a significant indicator value for stands with a penetration rate >23%, 1 of which was also an indicator for low amount of dead wood and 17 for high amount of dead wood. Five species had a significant indicator value for low amount of dead wood, and 16 species for high amount of dead wood (Table 2). Indicator species of the Red List class "critically endangered" were found only in categories with a high level of dead wood.

4. Discussion

Our study is among the first to quantify the effects of dead wood accumulation and canopy opening by bark beetle infestation and tree senility on saproxylic beetle assemblages in a large protected area. Assessment of the effects of natural disturbance is often complicated by insufficient spatial or temporal replication and control (Harborne et al., 2008). We minimized this problem by establishing a large number of sampling sites along a wide gradient of increasing penetration rate and total amount of dead wood. Increasing amounts of spruce dead wood and opening of the canopy both by bark beetle infestation had positive effects on the abundance of saproxylic beetles, including red-listed species, and on the composition of assemblages. This effect holds true when the analysis is controlled for elevation and habitat continuity.

4.1. Amount versus diversity of dead wood

One key problem in most field studies of saproxylic species based on survey data and using correlative analysis as in our study is that the effects of amount and diversity of dead wood on the abundance and richness of species cannot be separated because the two factors are highly correlated (Økland et al., 1996; Siitonen et al., 2000; Fig. S3). One earlier field study claimed to have found a greater influence of diversity than the amount of dead wood on the number of saproxylic beetles (Similä et al., 2003). A critical evaluation of the results of this study, however, shows that both variables were positively correlated with richness and had similar correlation coefficients. Experiments following the standards of classic biodiversity studies are needed to separate the effect of diversity and abundance (Hector et al., 1999). For practical purposes, however, knowledge that the amount of dead wood is a surrogate for the diversity of dead wood is useful, even if the mechanisms behind the correlation are unclear.

4.2. Abundance versus species richness of beetles

In our study, the increase of dead wood and canopy openness led to an increase in the abundance of saproxylic beetle species. Correcting the number of species by using individuals as covariate resulted in weaker effects of environmental variables on species richness. This supports the "more individuals hypothesis", i.e., sites with more resources are inhabited by more individuals and therefore also more species (Srivastava and Lawton, 1998). Although mostly ignored in previous studies, this hypothesis seems to be an important explanation for patterns in diversity of saproxylic beetles.

Many species respond to an increase in resources by a rapid increase in population, which also was true for the specialized and red-listed species in our study. This explanation applies to the many studies that found an increase in rare species outside of protected areas, when resources were created by management (Hyvärinen et al., 2006; Wikars, 2004). We found a positive response of saproxylic beetles to dead wood amount for both broadleaf and conifer specialists. An interesting example is *Ostoma ferruginea* (Table 2), which was rare in the pre-disturbed forest of the national park (Apfelbacher and Geiß, 2006). An abundance of >100 individuals of this species found in our samples has not been reported in any standardized sampling in Germany within the last 100 years. This species is associated with *Fomitopis pinicola*, the major fungus on dead wood of spruce. Another example is the Elateridae, *Ampedus auripes*, which is rare across Europe (Wurst and Kaupp, 1995). Populations of this species increased in our study area (to >300 individuals in our samples) after bark beetle infestation. Therefore, large-scale disturbance caused by bark beetles, if not followed by salvage logging, can restore population densities of rare saproxylic species.

4.3. Differences in host specialization and conservation status

The comparison of the explained variance for red-listed species with common species indicates that the former are more closely related to features of dead wood than the latter. Therefore, maintaining naturally disturbed protected areas with sufficient quantities of dead wood is an important conservation strategy for these species. Species typical of habitats with low amounts of dead wood in our study are mostly colonizers of thin dead trees (i.e., *Salpingus ruficollis, Xylechinus pilosus*), and some are considered pest species (*Xyloterus domesticus*, *Xyleborus dispar*). Furthermore, we found only a few species that are indicators for low amounts of dead wood. Our analysis of variance partitioning showed that our bark beetle predictor set had the highest positive effect on conifer specialists and generalists, with canopy openness also being important, particularly for conifer specialists. This finding supports the hypothesis that opening of the canopy by bark beetles across large areas leads to population increases of associated saproxylic species. In general, beetle species typical of more-open forests, such as dry pine or spruce, are often associated with open canopy con-

ditions, for example, those created by fire or wind (Duelli et al., 2002; Hyvärinen et al., 2006; Moretti and Barbalat, 2004). Interestingly, it has been shown that high canopy openness is favorable even for the establishment and growth of regenerated Norway Spruce (Nilsson et al., 2002). In contrast, the specialists of broadleaf trees were negatively affected by canopy openness in general, which can be explained by significant higher proportions of species feeding on fungi ($Chi^2 < 0.001$; Table 2; Fig. S7). For wood-rotting fungi, diversity is negatively affected by a rapid opening of the canopy (Bässler et al., 2010), which may be explained by drier wood conditions.

4.4. Thresholds for canopy openness and amount of dead wood

Our analysis discovered two splits for ordination scores: at 23% penetration rate and at 64 m^3 ha^{-1} amount of dead wood. The high number of indicator species for open (31 species) and dense forests (16 species) supports the view that two distinct communities exist with respect to openness: one community in open habitats with species associated with sunny conditions, e.g., *Judolia sexmaculata*, and one community occurring in dense stands, e.g., *Hedobia imperialis* (Möller, 2009; Table 2). For the amount of dead wood, however, the correlation of the second ordination axis with species numbers, the significant nestedness, and the rather low number of indicator species for low levels of dead wood suggest that the communities of saproxylic species become impoverished with low amounts of dead wood, but increase in species richness as the amount of dead wood increases. Thus, communities containing all species, including such specialists as *Ceruchus chrysomelinus* (Möller, 2009), need a minimum amount of dead wood.

Both thresholds with their confidence intervals are informative for developing guidelines for conservation. However, the calculation of ecological thresholds has been criticized from a theoretical point of view. A disadvantage of specifying thresholds is that individual species responses may be continuous without a sharp breakpoints (Lindenmayer and Luck, 2005; Müller et al., 2009a; Ranius and Fahrig, 2006). Furthermore, different thresholds have been found for different species and taxonomic groups (Moning and Müller, 2009; Økland et al., 1996; Fig. S7) and for the same species in different regions (Bütler et al., 2004). Independent of whether real ecological thresholds exist, the recognition of splits is useful to set targets for nature conservation. Such values are easily understood as benchmarks (Müller and Hothorn, 2004; Müller et al., 2009b; Villard, 2009). In our study, a "complete" community of saproxylic beetles is associated with clearly higher amounts of dead wood than occur in commercial forests (see Fig. 1). Furthermore, as pointed out by Drapeau et al. (2009), if a variable in a system falls below the defined threshold, this may be an important warning signal for managers.

4.5. Implications for managed and unmanaged forests

Disturbances can occur on large scales unexpectedly. The bark beetle outbreak in our national park was unanticipated, which explains the lack of a before-after-control impact design in our study. Therefore, our study should be regarded as a case study. Nevertheless, our results highlight general implications for montane habitats in Central Europe. For conservation-oriented management of commercial mixed montane forests, our data suggest two rather contrasting strategies of importance. In dense stands with less than around 20% canopy openness, dead wood of beech and fir, in particular, should be increased to at least 30–60 m^3 ha^{-1}, which would improve habitat quality for beetles specialized on broadleaf trees or associated with wood-decaying fungi. In open stands with more than 20–50% canopy openness, management should aim at increasing dead wood, particularly of conifers, to similar amounts. Such increases of dead wood in logged forests in both situations would support more complete saproxylic communities, including generally all species associated with high amounts of dead wood (Table 2).

For large protected areas, such as national parks, our study highlights the importance of bark beetle dynamics in the restoration of habitats that support many saproxylic species (Table 1, Fig. S8). The positive responses of abundance and composition of beetle assemblages to dead wood produced by bark beetle infestation suggest that saproxylic beetles benefited from natural dynamics in the national park over the last 20 years. Similar diversifying effects of natural disturbance have been shown for fire and windstorms (Agee, 1993; Bouget and Duelli, 2004; Hyvärinen et al., 2006; Noss et al., 2006). In contrast to logging, which also creates canopy openness, natural disturbances do not reduce the basic resource for saproxylic organisms: dead wood. Therefore, the disturbance effect of logging is short lived rather than self perpetuating (Hyvärinen et al., 2006).

Forest dynamics have evoked debates about "dead forests" and prompted calls for salvage logging (Noss and Lindenmayer, 2006). With salvage logging, the amount of dead wood would decrease, leading to "incomplete" assemblages of saproxylic species. Therefore, we recommend that nature be allowed to take its course in strictly protected areas such as national parks, with forests of the type studied here, and that the amount of dead wood within these protected areas be allowed to increase. Moreover, our results demonstrate that unmanaged areas or management by "benign neglect" (Zahner, 1992) can be quite successful in restoring natural forest dynamics, habitats, and the organisms dependent on forest structures. Such management is considerably less expensive than intensive management and has the additional advantage of creating the forest wilderness aesthetics that is of great interest to many human visitors (Müller and Job, 2009).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.06.024.

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Artikel III

Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns

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Abstract

Scolytids have been studied more than any other group of forest insects, but most investigations have been restricted to only a few pest species. This bias hampers our understanding of variation in abundance and pest status. Even the simple question whether the abundance of scolytids can predicted by the same independent variables as their pest status is still a matter of debate. To explore this issue, we estimated their abundance using non-attracting flight-interception traps set in a wide range of forests across Czech Republic, Germany, and France. Pest status was taken from current literature. As independent variables, we considered host range, host abundance, and several traits of the considered species in linear models using generalized least squares with a correlation structure derived from the phylogenetic tree of the beetles. Host range was calculated as the root phylogenetic diversity index. The variation in the abundance across scolytids was well explained by resource-related parameters (R^2 = 0.53). In contrast to abundance, the pest status was significantly related to species-specific traits, such as body size and maximum number of generations. However, the explained variance was much lower (R^2 = 0.19). Although our analysis showed that abundance and pest score follow different patterns, we stress the importance of monitoring all species using non-selective traps. Considering the increasing global trade and the rapidly changing climate, such a broad ecological monitoring is necessary to detect new interactions and/or invading species that may influence our forests ecosystems.

Key words: *Scolytinae*, root phylogenetic diversity index, invasive species, *Xyleborus saxesenii, Xyleborus germanus, Cyclorhipidion bodoanus.*

Introduction

In temperate and boreal forests, some species within the sub-family *Scolytinae* (Coleoptera) are important pest species attacking economically important forest trees (Lieutier et al., 2004). Scolytids have two fundamental feeding strategies, as xylomycetophagous (ambrosia) beetles and as phloeophagous (phloem-feeding) beetles (Beaver, 1979; Paine et al., 1997). Ambrosia beetles bore galleries into the wood or bark of host trees and cultivate there symbiotic *Ambrosiella* species (ascomycete fungi). Fungal infestation lowers the economic value of wood, particularly by causing undesirable color (Orbay et al., 1994). Therefore, chemicals are used to combat ambrosia beetles (Schwenke, 1974) - in Germany especially against *Xyloterus lineatus*. The phloeophagous beetle species kill trees directly by phloem girdling (Wermelinger, 2004). Phloem-feeders are associated with blue-stain fungi (e.g., *Ceratocystis polonica*, *Ophiostoma penicillatum*) and some of these even kill the trees (e.g., *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*). The most harmful phloeophagous beetles in Europe are *Ips typographus*, *Tomicus piniperda*, *Pityogenes chalcographus,* and *Ips acuminatus*, which contribute 50% of the yearly biotic damage in European forests (Schelhaas et al., 2003; Grégoire and Evans, 2004). Using chemicals against phloem feeders in standings trees is difficult and therefore only rarely applied (Schwenke, 1981).

Outbreaks often follow windthrows (Wermelinger, 2004), and recent changes in the climate have been linked to the overabundance of some of these species (Jönsson et al., 2007; Raffa et al., 2008). Such large-scale outbreaks evoked considerable public interest in commercial forests, but surprisingly also in protected areas (Martin et al., 2006; Fettig et al., 2007; Raffa et al., 2008). For example, *Ips typographus* has destroyed vast areas of mature spruce trees in the montane forests of the Bavarian Forest National Park, which changed the landscape dramatically (Müller et al., 2008). The administration of the national park decided against management of these areas to allow for natural processes of forest succession and

regeneration. This policy has led to the formation of a citizens' action group opposing the non-management strategy with intense and emotional discussions (Müller and Job, 2009).

Numerous institutions invest a considerable amount of time and money to monitor *Ips typographus* and other potential pest species using highly selective pheromone traps (Bussler, 2006; Grégoire and Evans, 2004; Wermelinger, 2004). Only one-third of the ~100 scolytids in central Europe, however, are classified as pests in at least one European country (Lieutier et al., 2004). Furthermore, studies with non-selective traps found that species may be abundant, but are not classified as pests. Some of them are invasive species that occur in central European forests since several decades (Bussler and Müller, 2004; Bussler, 2006). Nevertheless, such abundant species have the potential to become pests because climate change may induce new host–species interactions (Cudmore et al., 2010) and may affect interspecific interactions between scolytids, mites, and fungi (Paine et al., 1997; Hofstetter et al., 2007). In turn, such changes may change the pest status of species. Given the paucity of comparative studies on the abundance of scolytids, the issue of predicting the pest status of scolytids is still not settled. This evoked the general question of why some scolytids are abundant and why some of these species have become pests.

The occurrence and abundance of a phytophagous insect is constrained by the occurrence and abundance of the host plant (Quinn et al., 1998). Specialized species that use one rare host plant must therefore also be rare. In contrast, polyphagous insects that attack widespread and abundant host plants can become very common but may also remain rare due to other reasons (e.g., parasitoids, limited dispersal), leading to a triangular scatter between host and insect abundance (Hodkinson and Casson, 2000). Overall, occurrence and abundance of host plants as well as host range are among the important ecological and evolutionary drivers of phytophagous insects (Schoonhoven et al., 2005). The host range of insects has both a phylogenetic and an ecological component (Kelley and Farrell, 1998; Kergoat et al., 2005; Goßner et al., 2009). A species can attack hosts that occur within the distributional

range of the insect and that have similar mechanical (e.g., trichome) or chemical (e.g., certain alkaloids) defense strategies (Juniper and Southwood, 1986; Walling, 2008). This leads to two predictions. First, as defense strategies of host plants are often phylogenetically conservative, insects should attack hosts related to one another (Brändle and Brandl, 2006). However, if distantly related hosts have similar defense strategies, then also these species are often within the host range (Berenbaum, 1995; Wiklund and Friberg, 2009). Second, with an increasing range of an insect, more potential hosts occur within the distributional range and the number of host plants of phytophagous insects should increase with its distributional range.

Irrespective of the detailed processes, it is clear that host range and host distribution are important factors determining scolytid species abundance. With respect to the prediction of abundance and pest status of scolytids, this leads to the simple hypothesis that abundant species and perhaps also pest species have a broad host range with widespread and abundant hosts. To test this hypothesis, we estimated the abundance of scolytids by using non-attracting flight-interception traps and derived pest scores as well as data of host plants from the literature. Since most scolytids live on trees, we used data from country-wide forest inventories to quantify resource availability and to explore the importance of host abundance for scolytids. Finally, we modeled abundance and pest status considering various potential drivers, e.g., host range, feeding strategy, and the species traits body size and maximum number of generations.

Methods

Scolytid abundance and pest status

Our own broad literature survey combined with information retrieved from the Fauna Europaea version 2.2 (www.faunaeur.org) revealed that 109 species of scolytids have been recorded in Germany. For estimating abundance of as many species as possible from this list, we collected samples from 1,793 flight-interception traps. Traps were located from the

western border of the Czech Republic to Germany to western France (Fig. S1). Experience from field surveys, during which one of us counted scolytids by visual surveys (HB unpublished material), suggested that passive flight-interception traps lead to estimates of relative abundances that are comparable across species. However, flight-interception traps, as any other trap, may possess some presently unknown bias. Traps were set within the course of several projects from 1995 to 2009. All traps were set throughout the vegetation period, and therefore we sampled the full spectrum of scolytids irrespective of their phenology. These trap catches comprised 308,298 scolytid individuals representing 88 different species. Four of the species sampled by our traps were not listed as occurring in Germany (*Orthotomicus erosus*, *Cryphalus numidicus*, *Pityogenes bistridentatus,* and *Pityophthorus buyssoni* recorded with traps in France).

All specimens were identified to the species level by experts according to Balachowsky (1949), Grüne (1979), Schedl (1981), and Pfeffer (1994, 1995). The summed number of individuals of each species across all traps was used as the measure of abundance. The pest status of the collected species was scored according to the number of countries in Europe in which a species was assessed as a pest on the basis of questionnaires (Grégoire and Evans, 2004) and ranged from 0 to 16. The pest status in the three sample countries was also scored (0 to 3).

Hosts, resources, and traits

We compiled data from published resources on the host genera of the species attacked in the wild because most such host records are reported at this level (Brändle and Brandl, 2001; Table S1; for references, see Supplementary material). Names of host genera were used as provided in the literature. Note that some of these genera are nowadays ranked only as subgenera. The data listed in Table S1 form the basis to calculate a quantitative measure of host range (see below).

For all species, we compiled additional information from the literature (Table S4): 1) For as many species as possible collected in the traps, we calculated the resource availability (basal area in m^2) across Germany using the detailed information provided by the German National Forest Inventory (BWI2 from 2001; www.bundeswaldinventur.de). For four species (*Hylastinus obscurus, Xylocleptes bispinus, Phloeophthorus rhododactylus,* and *Thamnurgus varipes*), no such information for their hosts was available. After removing these four species and the four species trapped only in France, our list of species used in most statistical analyses dropped to 80 species. For each species, we summed the basal area of all host genera. This resource availability across species ranged from 365,584 to 301,025,012 m^2 basal area. 2) As a surrogate for the distributional range across Germany, we used the number of regions with records of the species, ranging from 0 to 18 (Köhler and Klausnitzer, 1998). 3) We obtained the maximum number of generations per year (0–3) from Pfeffer (1995). 4) As a measure of body size, we used the body length, ranging from 1.05 to 7.0 mm, from Schedl (1981) and Pfeffer (1995). 5) Each species was classified as a phloem feeder or an ambrosia feeder according to Pfeffer (1995).

Phylogenetic analyses of host range

A simple count of host taxa is not necessarily a meaningful measure of host range. For example, *Orthotomicus laricis* infests *Pinus, Picea,* and *Larix*, and *Polygraphus grandiclava* infests *Pinus* and *Picea* but also *Prunus* (Avtzis et al., 2008). Although both species attack the same number of host genera, the phylogenetic relatedness of the host genera clearly indicates that *Polygraphus grandiclava* has a broader host range than *Orthotomicus laricis* (Symons and Beccaloni, 1999). For a phylogenetic measure of host range, we therefore estimated an approximate phylogeny of the host genera. For this we retrieved 70 sequences of the ribulose-bisphosphate carboxylase (*rbcL*) gene deposited in GenBank, using *Osmunda regalis* as outgroup. For seven genera, no sequences were available. In these cases, we selected a species

from the closest related genus (supplementary material Table S2). To construct a phylogenetic tree, we first selected an appropriate evolutionary model using MEGA5 (Tamura et al., 2011). The models with the lowest score of the Bayesian information criterion was considered to describe the substitution pattern the best. Heterogeneity of evolutionary rates among sites may be modeled by using a discrete gamma distribution with five rate categories and by assuming that a certain fraction of sites are evolutionarily invariable. All positions containing gaps and missing data were eliminated for this analysis, leading to 513 positions in the final dataset. This analysis selected a Tamura 3-parameter model (Tamura, 1992) with a rate heterogeneity (shape parameter 0.314), which we used for all further other analyzes. We then used the maximum-likelihood criterion and the selected evolutionary model to estimate a phylogenetic tree (log-likelihood = −4329.63).

A simple measure of host range that includes phylogenetic relatedness is the total path length of the subtree comprising all host genera of a particular insect species (= phylogenetic diversity index). However, this does not allow inclusion of monophagous species. Therefore, we used the root phylogenetic diversity (Root PD) index developed by Symons and Beccaloni (1999). First, we calculated the phylogenetic diversity index for all species with at least two host genera, and we added to this value the sum of branch lengths along the shortest path from the basal node of the minimum inclusive clade to the root. Second, for monophagous species, we calculated the shortest path from the tip to the root. Low values of Root PD indicate a narrow host range, and high values indicate a broad host range.

To improve the understanding of the variation in scolytid species of host genera, we modeled species richness of those 26 host genera used already in a previous study across all insects (Brändle and Brandl, 2001) by resource availability, the time span since the last glaciation in which a host genus was known to occur in central Europe (postglacial occurrence), and the number of host species within a genus (taxonomic isolation). The latter two variables were extracted from Brändle and Brandl (2001). Host genera, however, may not

form independent data points; therefore, we corrected for phylogenetic relatedness and used a linear model using generalized least squares (GLS) with a correlation structure derived from the phylogenetic tree of host genera (see above; Pagel 1999). Thereby Pagel's λ was optimized by selecting the model maximizing the likelihood (Freckleton et al., 2002). Pagel's λ indicated the degree of phylogenetic constraints from 0 (no) to 1 (fully constrained). Manual fixation of λ allows one to check the influence of selecting a specific λ on the statistical outcome.

To test whether host choice in scolytids is phylogenetically constrained and therefore conservative, we analyzed the deviation of the observed Root PD from the expectation that species select host or hosts at random using various null models (Gotelli, 2000). First, we estimated the expected Root PD for each host range from 2 to 19 hosts, selecting hosts randomly from the host phylogeny. From 200 runs, we calculated the mean and the associated confidence limits of the expected Root PD that fixes the number of hosts used by each species but which destroys the variation in species richness between host genera. Second, we randomized the matrix of host records (69 hosts and 113 species), keeping the number of hosts used by a beetle species as well as the number of species on each host genus fixed. For these randomizations, we used the function *randomizeMatrix* with the method *independentswap* with the add-on package *picante* in R. We simulated 200 randomized matrices and calculated from the simulations the expected Root PD and the associated standard error. Finally, we calculated the effect size (observed–expected)/standard error. A negative effect size indicates that the expected size is larger than the observed size and thereby that the phylogenetically corrected host range is smaller than expected by chance.

To gain a deeper understanding of the drivers for Root PD, we analyzed the Root PD relationship to resource availability, distributional range, body size, number of generations, and feeding strategy. However, in such an analysis, data points (individual scolytid species) might not be independent (Felsenstein, 1983; Garland et al., 1992), which inflates the degrees

of freedom (see above, where we corrected for relatedness of hosts). Therefore, we corrected for phylogenetic relatedness of beetles and used a linear model using generalized least squares (GLS) with a correlation structure derived from the phylogenetic tree of scolytids using again Pagel's λ (Pagel 1999). However, for scolytids, it was not possible to select sequences; therefore, we modified an existing tree and estimated branch length from fossil records. The information provided by Hunt et al. (2007) was used as the topological backbone for our phylogenetic tree. We expanded this tree with information provided in Cognato and Vogler (2001) and the taxonomic information of Grüne (1979) using facilities in the add-on package *picante* (Kembel et al., 2010). Finally, we used 15 calibration points affirmed by records of scolytids in amber (Petrov and Perkovsky, 2008; Kirejtshuk, 2009; Kirejtshuk et al., 2009) for dating certain nodes of the phylogenetic tree (Table S3). We estimated the branch length with the function *bladj* in *picante* (Fig. S2).To test our hypothesis, we modeled the abundance and the pest scores using GLS incorporating phylogenetic relatedness of beetles by resource availability, Root PD, distributional range, body size, number of generations, and feeding strategy as dependent variable. To meet the assumptions of the models, we $\log_e$-transformed resource availability, the number of congeneric species, and the pest scores.

Results

Our compilation of records of the hosts of 113 central European scolytids revealed that the four most species-rich host genera were conifers (Fig. 1): *Pinus* (59), *Picea* (38), *Abies* (22), and *Larix* (17). Broadleaf genera harbored fewer species of scolytids; the four most species-rich broadleaf genera were *Quercus* (16), *Ulmus* (13), *Carpinus* (11), and *Fagus* (10). Pagel's λ indicated a considerable degree of phylogenetic constraint of species richness of scolytids across host genera (Table 1). Of the three independent variables, resource availability had the most significant impact on the species richness of scolytids (Table 1). The analysis was robust with respect to the selection of λ (Table 1).

Four of the 113 scolytid species (109 known to occur in Germany plus the four recorded in the traps from France) were invasive species: *Xyleborus germanus*, *Cyclorhipidion bodoanus*, *Xyleborus alni*, and *Gnathotrichus materiarius.* The four scolytid species with the highest number of host genera were *Xyleborus saxesenii* (19), *Scolytus rugulosus* (17), *Xyleborus dispar* (16), and *Scolytus mali* (13). The most abundant species was *Xyleborus saxesenii*. The invasive scolytids *Xyleborus germanus* and *Cyclorhipidion bodoanus* were two of the six most abundant species (Fig. 2).

The number of host genera used by each species was well correlated to the phylogenetic measure of host range, Root PD ($r = 0.87$; Fig. S3a). This correlation was expected because the path length along a tree increases with the number of hosts, even for randomly selected host species. However, for most species, the Root PD values were smaller than the expected value irrespective of the null model. Therefore both types of analyses using null models indicated some conservatism in host choice of species (Fig. S3b). Modeling the Root PD by distribution, maximum number of generations, body size, and feeding strategy revealed that a broad host range is correlated mainly by a large distribution, and the host range of ambrosia feeders is broader (Table 2). The estimate of Pagel's λ was 0.22, which indicated a phylogenetic signal in the variation of Root PD across species of scolytids. Modeling of the abundance of scolytids using various independent variables and taking phylogenetic relatedness between beetles into account allowed an explanation of 53% of the variation in abundance (Table 3, Fig. 3). The estimate of Pagel's λ was, however, 0, which indicated no phylogenetic signal in the variation of abundance across species of scolytids. All variables except the maximum number of generations within a year showed significant partial regression coefficients. As expected, the abundance increased with the available resources, Root PD, and distribution, and decreased with body size. Finally the model showed that the abundance of phloem feeders is lower than the abundance of ambrosia feeders. The parameter estimates for standardized variables suggested that resource availability and Root PD have the

strongest influence on the abundance. Fixing Pagel's λ to 1 had no impact on our conclusions (results not shown).

The results for central European and whole European pest scores were similar. The pest score increased with increasing maximum number of generations and with increasing body size (Table 3). The R^2 for pest score was considerably lower than that for abundance, with values around 20% (Table 3). The estimate of Pagel's λ was 0.34 for Pest score Europe and 0.13 for Pest score central Europe, which indicates some phylogenetic signal. The results suggest that abundance of scolytids follows different drivers than the pest status. The abundance is driven more by resource availability, and the pest status is driven by species traits. Again, fixing Pagel's λ to 0 or 1 had no impact on the general conclusions (results not shown).

Discussion

Number of scolytids on host genera

We found considerable variation in the number of scolytids recorded on various hosts as well as in the number of hosts attacked by various scolytids. The possible reasons for such differences in richness of phytophages across hosts have been extensively discussed (Kennedy and Southwood, 1984). Brändle and Brandl (2001) summarized the three major hypotheses explaining the species richness on plant genera: (1) The *species-area hypothesis* predicts that the species richness of phytophagous insects should increase with abundance and distribution of their host species. (2) The *geological time hypothesis* acknowledges that phytophagous insects accumulate on a given host when the host species occurs within a given area, and therefore host species that have been in a particular area for a long time should have assembled more phytophages than host species that arrived recently (Strong et al., 1984). (3) The *taxonomic isolation hypothesis* assumes that the host range of insects is constrained by the host phylogeny, and therefore tree species with co-occurring relatives should have more

phytophagous species than taxonomically isolated trees (Strong et al., 1984). Our results confirm that the host area (Fig. 4) and probably the time a host species occurred in Europe contribute to species richness; therefore, in this respect, scolytids are like other insects (Brändle and Brandl, 2001; Strong et al., 1984).).

Scolytids on non-native hosts

Non-native plants are often depleted in phytophages (for scolytids see Pfeffer, 1995). However, the degree of depletion is dependent on the presence or absence of congeneric species as well as on the chemical components of the plants, and a trend to more-generalized species on non-native plants has been observed (Degomez and Wagner, 2001; Brändle et al., 2008; Bertheau et al., 2009; Goßner et al., 2009). Of the four non-native tree genera, only on *Robinia* were much fewer scolytids recorded than expected from the regression of species number versus resource availability, although *Robinia* was introduced to Europe around 1602 (Mayer, 1977). In contrast, *Pseudotsuga* was introduced 225 years later in 1827 (Knoerzer and Reif 2002), but the number of scolytids was already close to the expected number of species (Fig. 4). According to our phylogenetic tree, *Pseudotsuga* is closely related to *Larix*, whereas *Robinia* is only distantly related to the other few Fabaceae that are also hosts for scolytids (Fig. 1). Furthermore, these species are attacked by a small number of scolytids and are no tree species. Hosts with close relatives from the same life form (e.g. tree) in their new distribution area, however, accumulate insects rather quickly (Goßner et al., 2009). The other non-natives in our list of hosts (*Juglans* and *Castanea)* occur in Europe at least since Roman times and are therefore classified as archaeophytes. Therefore, it is not surprising that the number of scolytids attacking these two species was close to the expected number from the regression (see also discussion of species richness of hosts).

Phylogenetic host range

Including phylogenetic relatedness of host species into a measure of host range (Novotny and Basset, 2005; Weiblen et al., 2006) opens the opportunity for a sophisticated test for constraints of host selection. We found that phylogenetic host ranges are smaller than expected by chance, and that even closely related species may have very different host ranges, which indicates that the processes and factors influencing whether a species is a specialist or generalist is a phenomenon on the species level. First of all, phytophages attacking host plants have to overcome certain defense strategies of the plants (Berenbaum, 1995). Furthermore, the possibilities of the plants to defend against herbivores depend on the feeding strategy of the insects (Schoonhoven et al., 2005). Therefore, mining or galling insects that live within the plant are involved in closer interactions with the plant than ectophages. Consequently, mining and galling insects are often more specialized than ectophages (Novotny et al., 2010). Bark beetles in general live within the cambium but also within the wood, and we expect that this group of insects show a specialization in between that of ectophages and mining or galling insects. Each scolytid species has generally one of the two feeding strategies; a mixed strategy is known only for two European species (Kirisits, 2004). Most ambrosia beetles breed in dead wood, with the larvae feeding on *Ambrosiella* species. In contrast, phloem feeders live mostly in the cambium and feed on phloem, thereby initiating defense actions of the host (Lieutier, 2007). Therefore, as expected from the work of Beaver (1979), the Root PD was larger for ambrosia feeders (Table 2). Furthermore, the effect size of phylogenetic host range was −1.9 for ambrosia feeders and −2.4 for phloem feeders.

Drivers of abundance

The abundance of scolytids increased with resource availability and host range, and decreased with body size. The influence of these three variables is expected considering general ecological considerations (Quinn et al., 1998). Species having a small resource basis must be

rare, whereas species with a large resource basis can be abundant, which leads to a triangular scatter of resource availability and abundance, as clearly shown by our data (Fig. 3). A similar argument is put forward for the relationship between abundance and body size. Large species are rare, whereas small species can be common. Macroecologists often explain this triangular scatter using arguments from population dynamics (Hodkinson and Casson, 2000; Brown, 1995; Brown et al., 2004). Large species need more resources and therefore build up smaller population sizes within a given area (Brown, 1995). For insects, we feel that this argument is a bit shaky because all insects are relatively small, and the population size of even the larger scolytid species may reach large numbers within a small area (see Wermelinger, 2004). Instead, we argue that small scolytid species, such as *Pityogenes chalcographus* and *Xyleborus germanus,* can colonize trunks but also rather small twigs, leading to an increase in the resource availability that is not captured by the measure of resource availability used in the statistical analysis.

In general, host range and resource availability are not independent. However, in our data set, the two variables were not correlated ($R^2 = 0.01$), and multivariate analysis clearly showed that both variables contribute independently to abundance. Thus, our finding that an increasing host range increases abundance does not mean that polyphagous species have generally more resources. Polyphagous species must have traits that help them to build up high population sizes.

Drivers for pest scores

Pest scores increased with body size, which is opposite to our findings for abundance. Large species tend to be more restricted to woody structures with larger diameters. For example, *Ips typographus* regularly attacks only mature spruce trees with basal diameters of > 25 cm (Wermelinger, 2004). A similar situation has been observed for *Dendroctonus* species acting as pests in North America (Raffa et al., 2008). With their focus on larger diameters, these

species quickly get into competition with foresters for valuable wood, which explains the increasing pest score with body size.

The second parameter that was significantly correlated with the pest score was the maximum number of genera within a year. Those species that are able to increase their population numbers rapidly under suitable conditions, as in warm years or after windblows, can boost their population size to numbers that allow them also to overwhelm the defense strategy of vital trees (Jönsson et al., 2007). Several small, invasive, and abundant species (e.g., *Xyleborus germanus*) have only one generation per year, which may result in lower population peaks with lower possibilities to overwhelm vital trees in concentrated attacks**.**

Body size and number of generations may also be indicators for interspecific competition ability. However, even evidence on interspecific competition of the well-investigated species *I. typographus* and *P. chalcographus* is low (Hedgren and Schroeder, 2004). Furthermore, information on resource partitioning of scolytids is scarce. Only for a few species do we have evidence that some related species differ in their phonological niche (Martikainen, 2001).

Conclusion

Our analysis across central European forests demonstrates that the abundance of scolytid species is driven by resource availability and related traits, such as host range. In contrast, pest species are driven by species traits, such as body size and the maximum number of generations. Abundance can be explained well by ecological information on the species, but the pest score cannot. The most abundant species in central European forest are generally not the focus of pest research, and two of the six most-abundant species are invasive species. Although our analysis showed that abundance and pest score follow different patterns, we advocate a monitoring of all species using non-selective traps. Considering the increasing

global trade and the rapidly changing climate, such a broad ecological monitoring is necessary to detect new interactions and/or invading species that have the potential to become pest species.

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Figure Captions

Fig. 1: UPGMA tree of 69 host genera of scolytids in central Europe and the number of scolytid species. Red, gymnosperms; blue, angiosperms. The tree is based on sequence divergence of *rbcL* genes and genetic distances calculated using Tamura's 3-parameter method with the rate variation among sites modeled with a gamma distribution (shape parameter 0.311) with a pair-wise deletion of missing values.

Fig. 2: Species–rank abundance curve of 80 scolytid species from 1,793 flight-interception traps in the Czech Republic, Germany, and France. Triangles, ambrosia feeders; circles, phloem feeders; red-filled symbols, classified as pests in the Czech Republic, Germany, and France (C/G/F); brown-filled symbols, classified as pests in other European countries. An asterisk indicates invasive species. The most-abundant species and some species with management relevance are labeled.

Fig. 3: Scatterplots of the relationships between the abundance of 80 scolytids and several variables that are expected to influence abundance. Root PD: root phylogenetic diversity index.

Fig. 4: Scatterplot of the number of scolytid species of a host genus in central Europe *versus* resource availability in Germany. Resource availability was estimated from the basal area taken from the nation-wide forest inventory in 2001. The line is plotted using the parameters in Table 1 with $\lambda = 0.76$ and using the means for postglacial occurrence and number of congeneric species. The given R^2 is for the raw scatter of the data for comparison with published relationships; non-native tree genera are in bold.

Table 1: General least-square estimates for the parameters used to model the number of scolytid species on 26 tree and shrub genera (see Fig. 1). The estimates of the parameters using Pagel's $\lambda = 0.76$ were calculated using the phylogenetic tree of the 69 host genera (for an ultrametric version of the tree see Fig. 1); the estimate for standardized variables is also given for this analysis in the second column to allow a direct comparison of the slopes. $\lambda = 0$, no phylogenetic signal; $\lambda = 1$, full phylogenetic signal. ** $p < 0.01$, *** $p < 0.001$.

	Estimates			
	$\lambda = 0.76$; $R^2 = 0.53$		$\lambda = 0$; $R^2 = 0.53$	$\lambda = 1$; $R^2 = 0.50$
Intercept	−1.35	1.79	−2.47	−0.85
Variable				
Resource availability [m^2]	**0.21 ** **	**0.49**	**0.29*** **	**0.18*** **
Postglacial occurrence [year]	3.32×10^{-5}	0.13	4.16×10^{-5}	2.42×10^{-5}
Congeneric species [n]	−0.16	−0.13	0.27	−0.30

Table 2: General least-square estimates for the parameters used to model Root PD. The feeding strategy is a dummy variable with a value of 0 for ambrosia feeders and a value of 1 for phloem feeders. The first column of numbers presents raw estimates of the parameters using Pagel's λ calculated with the phylogenetic tree of the beetle species (Fig. S2) for each dependent variable, and the second column presents raw estimates for standardized variables that allow a direct comparison of the slopes. + p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001.

		Root PD	
		Estimates	
		$\lambda = 0.22$; $R^2 = 0.33$	
Intercept		0.26	0.32
Distribution [n]		**6.93×10^{-3} ****	0.03
Maximum number of generations [n]		-4.00×10^{-3}	-2.3×10^{-4}
Body size [mm]		-1.38×10^{-2}	-1.58×10^{-2}
Feeding [Ambrosia/Phloem]	0/1	**−0.14 *****	−0.14

Table 3: General least-square estimates of the parameters used to model abundance and pest scores considering all of Europe or considering Germany, Czech Republic. and France, of 80 scolytid species (log_e-transformed). The feeding strategy is a dummy variable with a value of 0 for ambrosia feeders and a value of 1 for phloem feeders. The first column of numbers presents raw estimates of the parameters using Pagel's λ calculated with the phylogenetic tree of the beetle species (Fig. S2) for each dependent variable, and the second column presents raw estimates for standardized variables that allow a direct comparison of the slopes. + $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

		Abundance		Pest score Europe		Pest score central Europe	
		$\lambda = 0$; $R^2 = 0.53$		$\lambda = 0.34$; $R^2 = 0.25$		$\lambda = 0.13$; $R^2 = 0.19$	
Transformation		Estimates					
Intercept		−7.12	5.69	−0.77	1.43	0.33	0.26
Resource availability [m^2]	log_e	**0.56 *** **	1.03	−0.19	−0.34	−0.05	−0.09
Root PD		**8.66 *** **	1.02	−1.55	−0.18	−0.63	−0.07
Distribution [n]		**0.11 ***	0.59	0.04	0.23	0.01	0.07
Maximum number of generations [n]		0.76+	0.44	**1.55****	0.91	**0.26***	0.15
Body size [mm]		**−0.58 ***	−0.67	**0.99*****	1.14	**0.12***	0.14
Feeding [Ambrosia/Phloem]	0/1	**−1.58 ***	−1.58	−0.33	−0.33	−0.16	−0.16

Fig. 1

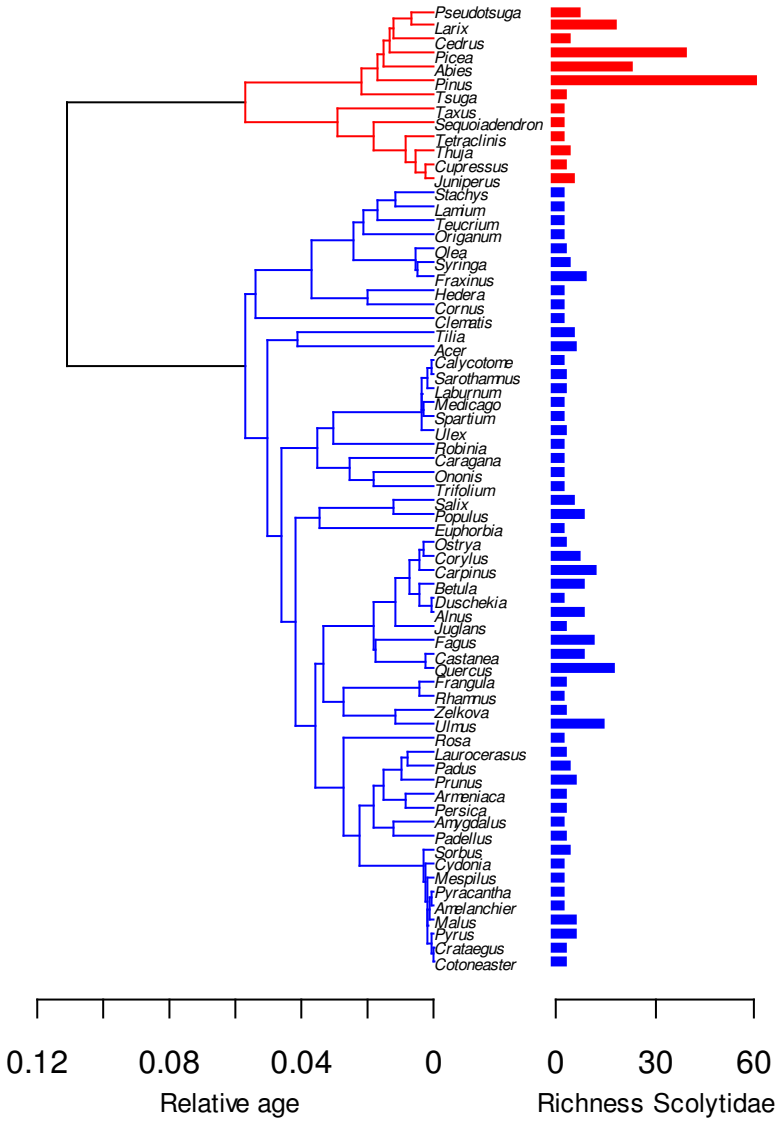

Pseudotsuga
Larix
Cedrus
Picea
Abies
Pinus
Tsuga
Taxus
Sequoiadendron
Tetraclinis
Thuja
Cupressus
Juniperus
Stachys
Lamium
Teucrium
Origanum
Olea
Syringa
Fraxinus
Hedera
Cornus
Clematis
Tilia
Acer
Calycotome
Sarothamnus
Laburnum
Medicago
Spartium
Ulex
Robinia
Caragana
Ononis
Trifolium
Salix
Populus
Euphorbia
Ostrya
Corylus
Carpinus
Betula
Duschekia
Alnus
Juglans
Fagus
Castanea
Quercus
Frangula
Rhamnus
Zelkova
Ulmus
Rosa
Laurocerasus
Padus
Prunus
Armeniaca
Persica
Amygdalus
Padellus
Sorbus
Cydonia
Mespilus
Pyracantha
Amelanchier
Malus
Pyrus
Crataegus
Cotoneaster
0.12
0.08
0.04
0
Relative age
0
30
60
Richness Scolytidae

Fig 2

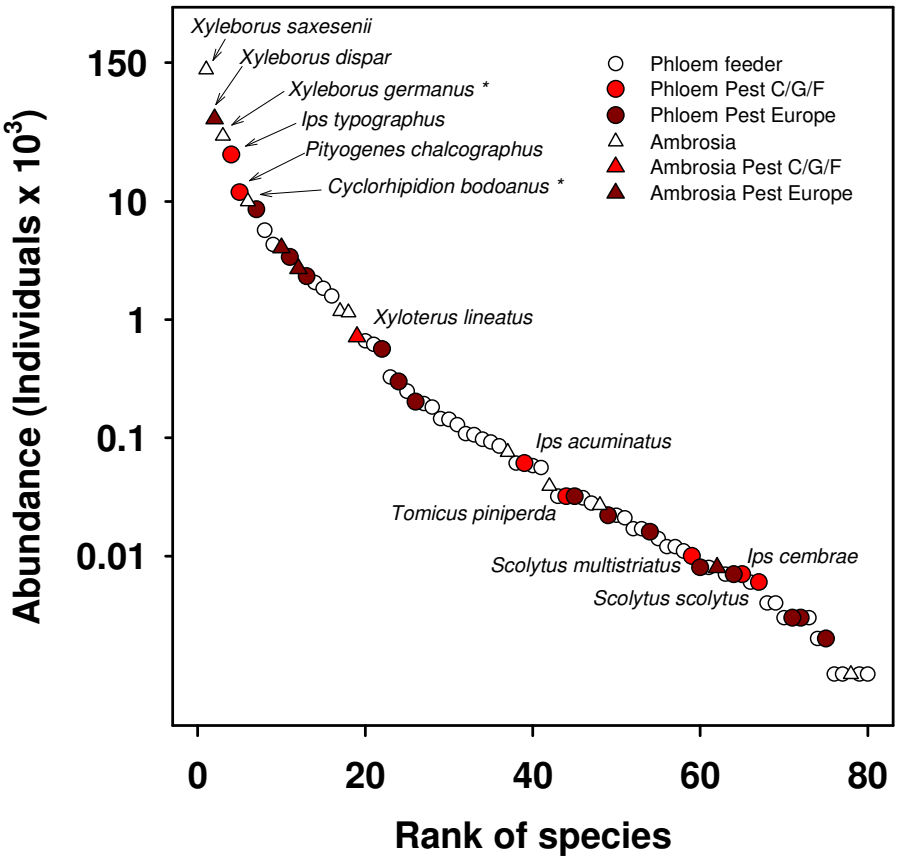

Xyleborus saxesenii
Xyleborus dispar
Xyleborus germanus *
Ips typographus
Pityogenes chalcographus
Cyclorhipidion bodoanus *
Xyloterus lineatus
Ips acuminatus
Tomicus piniperda
Scolytus multistriatus
Ips cembrae
Scolytus scolytus
Phloem feeder
Phloem Pest C/G/F
Phloem Pest Europe
Ambrosia
Ambrosia Pest C/G/F
Ambrosia Pest Europe
Abundance (Individuals x 10^3)
150
10
1
0.1
0.01
0
20
40
60
80
Rank of species

Fig 3

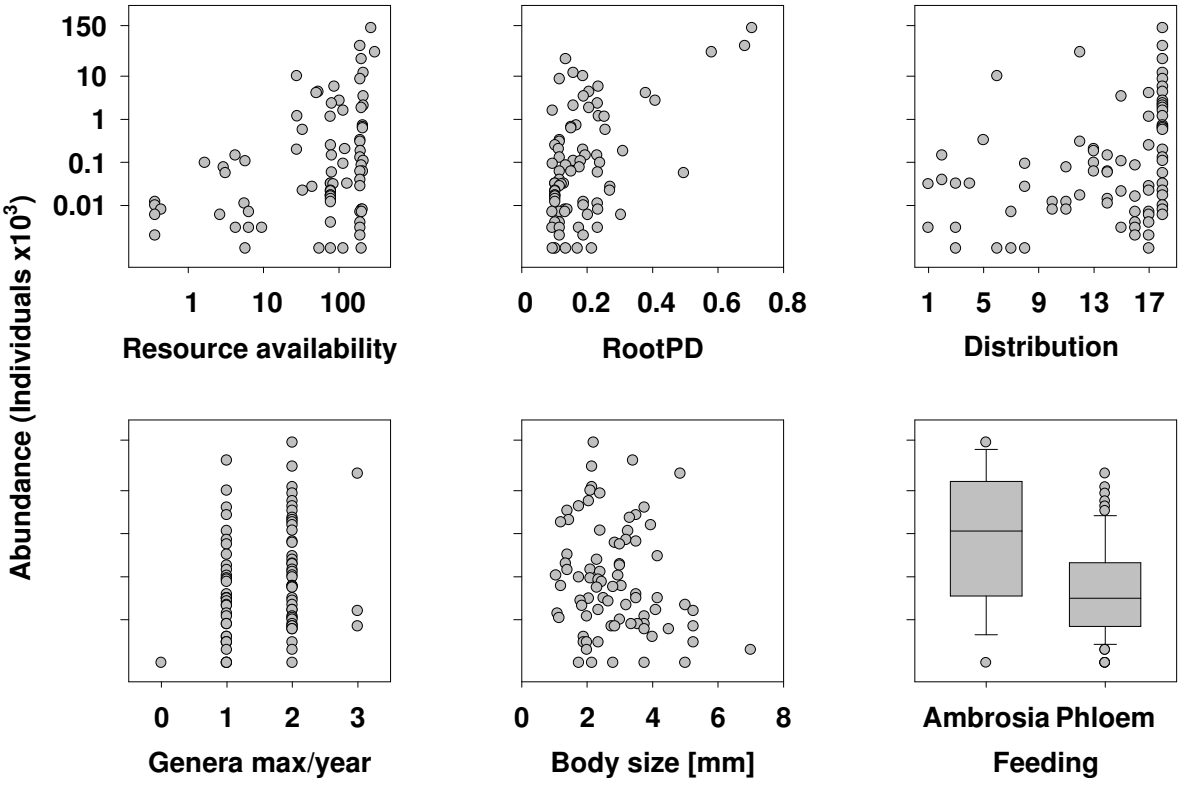
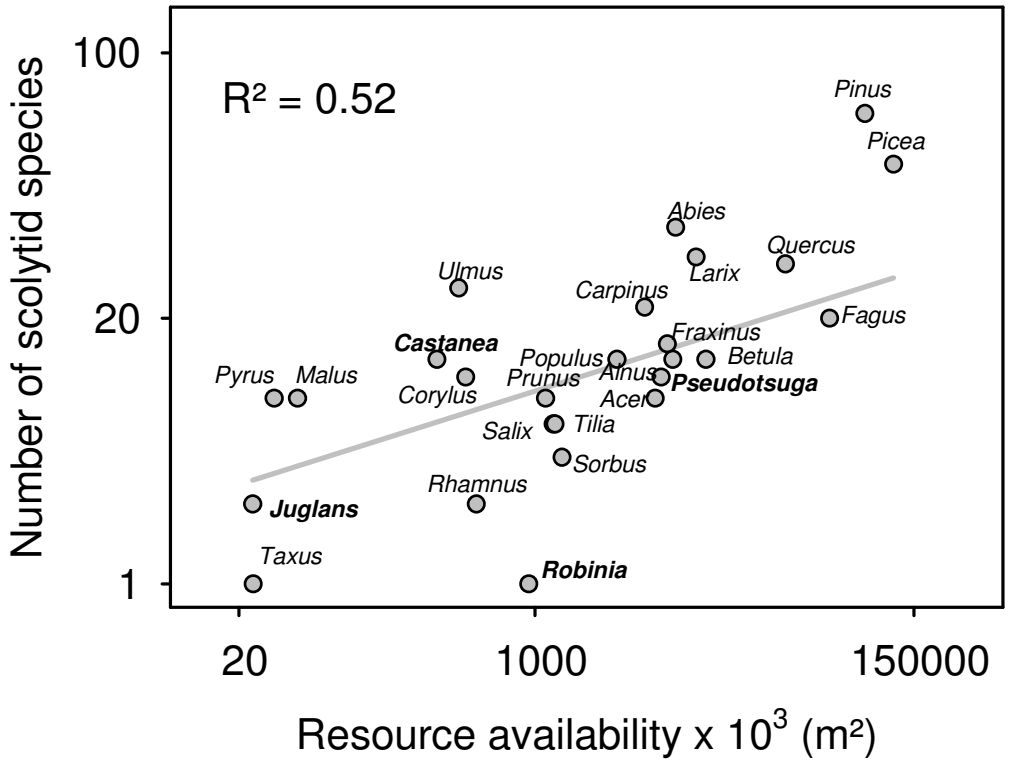

Abundance (Individuals x10^3)
150
10
1
0.1
0.01
1
10
100
Resource availability
0
0.2
0.4
0.6
0.8
RootPD
1
5
9
13
17
Distribution
0
1
2
3
Genera max/year
0
2
4
6
8
Body size [mm]
Ambrosia
Phloem
Feeding

Fig. 4


Number of scolytid species
100
20
1
R² = 0.52
Pinus
Picea
Abies
Quercus
Larix
Ulmus
Carpinus
Fagus
Fraxinus
Castanea
Populus
Betula
Pyrus
Malus
Prunus
Alnus
Pseudotsuga
Corylus
Acer
Salix
Tilia
Sorbus
Rhamnus
Juglans
Taxus
Robinia
20
1000
150000
Resource availability x 10³ (m²)

Supplementary material: Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns

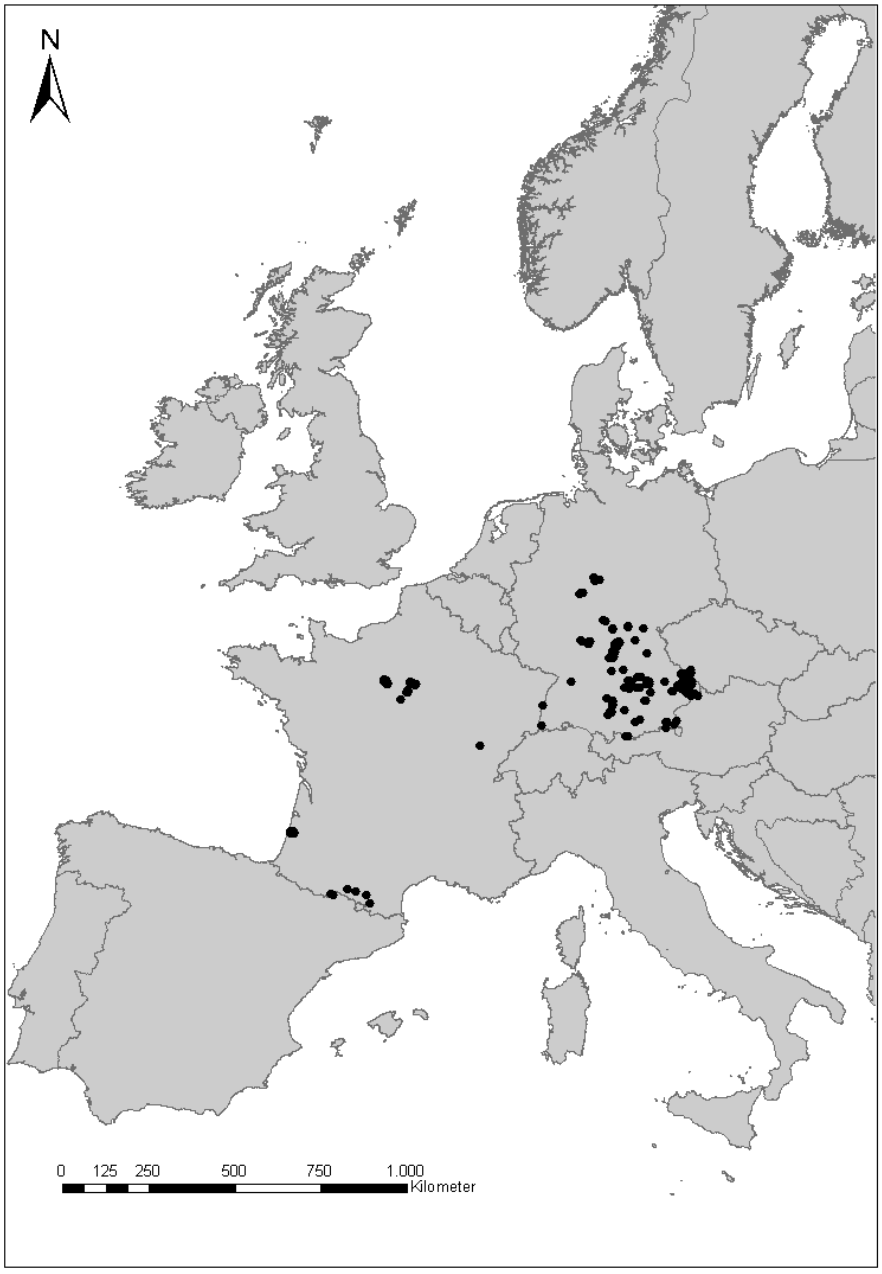


Fig. S1: Locations of the 1,793 flight-interception traps.

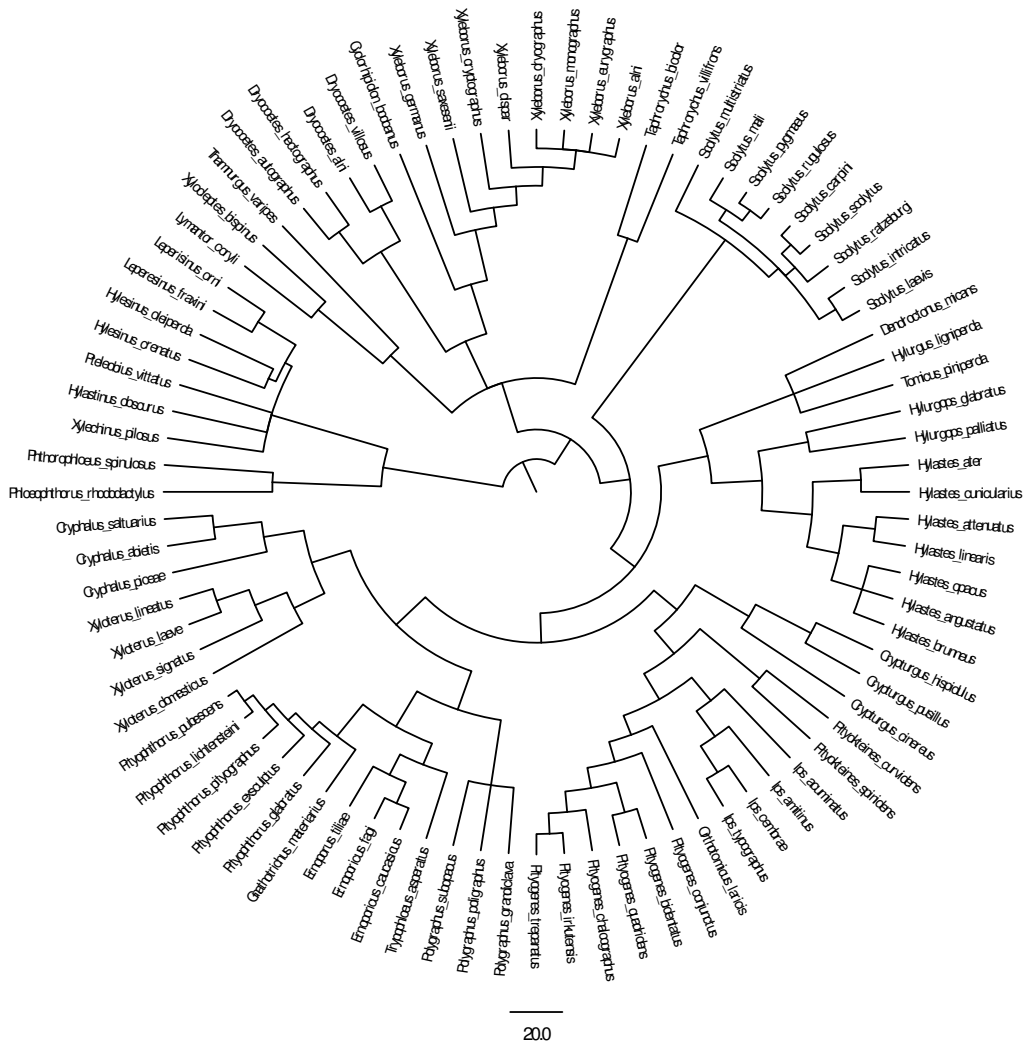


Fig. S2: Phylogeny of scolytid species. The phylogenetic tree is based on Hunt et al. (2007), further information within genera *Ips* spp., *Pityogenes* spp., and *Pityokteines* spp. were obtained from Cognato and Vogler (2001) and from taxonomic information (Grüne, 1979). Calibration was conducted with records of scolytids in amber taken from Kirejtshuk (2009) and Kirejtshuk et al. (2009); see Tab. S3.

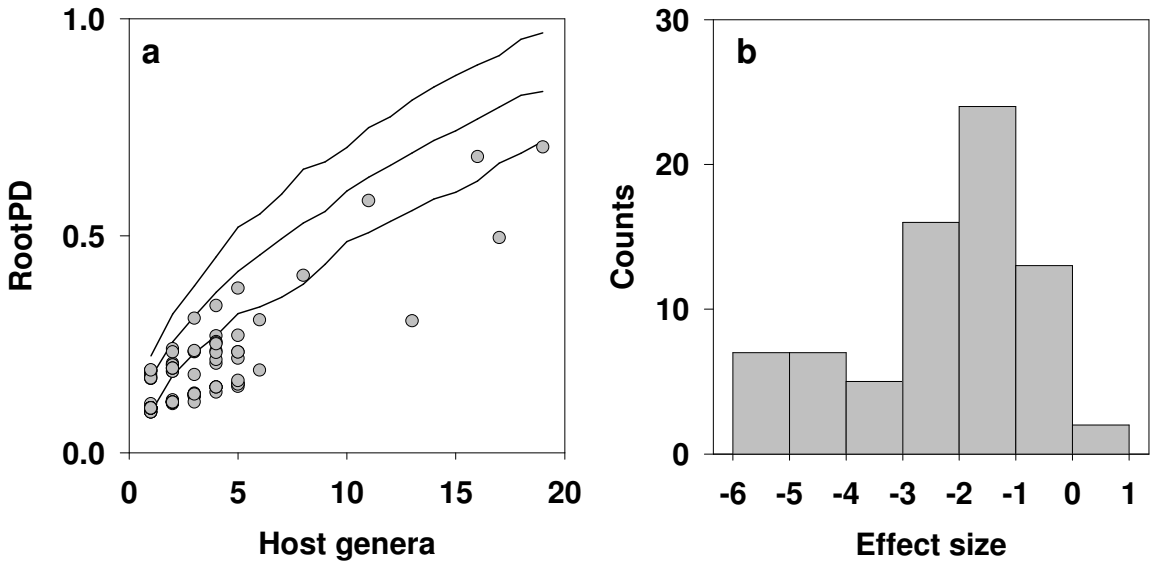


Fig. S3: (a) Deviation of the observed phylogenetic host range from a random expectation for scolytid species with 2–19 hosts. For each host range, hosts were selected randomly from the tree (200 runs). (b) Histogram of effect size (observed–expected)/standard error for randomization of the matrix of host records, keeping the number hosts used by a beetle species as well as the number of species on each host genus fixed. A negative effect size indicates that the phylogenetically corrected host range is smaller than expected by chance.

Table S1: Host genera of 109 scolytid species occurring in Germany and four species found only in traps from France.

See excel file Table S1

Table S2: Sequences used to construct the phylogeny of 69 host genera of scolytids in central Europe using the outgroup *Osmunda regalis*. Asterisks indicate genera for which no sequences were available; in these cases, sister genera were selected [genus (sister genus)].

Host genus	Representative species	Genbank No.	Sequence length (bp)
Picea	*Picea pungens*	AF456382.1	1409
Pinus	*Pinus cembra*	DQ353720.1	1436
Larix	*Larix laricina*	AF479878.1	1320
Abies	*Abies nordmanniana*	AB029654.1	1331
Quercus	*Quercus multinervis*	AY263938.1	1381
Acer	*Acer pseudoplatanus*	DQ978425.1	1391
Betula	*Betula nigra*	L12634.2	1402
Carpinus	*Carpinus betulus*	AY263928.1	1381
Cornus	*Cornus sericea*	AY725857.1	1401
Fagus	*Fagus sylvatica*	L13340.2	1345
Hedera	*Hedera helix*	FJ395559.1	598
Juniperus	*Juniperus communis*	AY988260.1	1283
Ulmus	*Ulmus americana*	AF500337.1	1409
Prunus	*Prunus spinulosa*	AF411503.1	1398
Pyrus	*Pyrus pyrifolia*	GU363809.1	703
Malus	*Malus baccata*	GU363810.1	703
*Padus**	*Prunus padus*	AF411485.1	1398
*Persica**	*Prunus persica*	AF411493.1	1398
Rosa	*Rosa woodsii*	U06824.1	1398
Sorbus	*Sorbus scopulina*	U06827.1	1398
Cotoneaster	*Cotoneaster horizontalis*	GU363807.1	703
Crataegus	*Crataegus columbiana*	U06799.1	1398
*Laurocerasus**	*Prunus laurocerasus*	U06809.1	1398
Amelanchier	*Amelanchier alnifolia*	U06793.1	1398
*Armeniaca**	*Prunus armeniaca*	AF411489.1	1398
Rhamnus	*Rhamnus cathartica*	L13189.2	1398
Taxus	*Taxus baccata*	EF660721.1	1321
Castanea	*Castanea sativa*	AF500363.1	1407
Corylus	*Corylus avellana*	AY263929.1	1381
Zelkova	*Zelkova serrata*	D86317.1	1290
*Sarothamnus**	*Cytisus scoparius*	Z70086.1	1368
Spartium	*Spartium junceum*	Z70102.1	1368
Ulex	*Ulex eurpaeus*	Z70111.1	1368
Laburnum	*Laburnum anagyoides*	Z70077.1	1368
Calicotome	*Calicotome villosa*	Z70089.1	1368
Fraxinus	*Fraxinus chinensis*	DQ673301.1	1434
Olea	*Olea europaea*	DQ673304.1	1428
Syringa	*Syringa vulgaris*	DQ673303.1	1434
Thuja	*Thuja plicata*	AF127428.2	1399
Tetraclinis	*Tetraclinis articulata*	L12576.2	1410
Cupressus	*Cupressus gigantea*	AY988246.1	1297
Sequoiadendron	*Sequoiadendron giganteum*	AY056580.1	1394
Frangula	*Frangula alnus*	EU676982.1	607
Clematis	*Clematis montana*	FJ449855.1	1393

Alnus	*Alnus glutinosa*	EU644678.1	1398
Populus	*Populus euphratica*	AB012778.1	1398
Salix	*Salix alba*	AB012780.1	1398
Tilia	*Tilia americana*	AF022127.1	1428
Pseudotsuga	*Pseudotsuga menziesii*	AY664856.1	1292
Tsuga	*Tsuga canadensis*	AY056581.1	1428
Caragana	*Caragana frutex*	FJ537234.1	1420
Juglans	*Juglans nigra*	U00437.1	1428
Cedrus	*Cedrus deodara*	AF456381.1	1428
Robinia	*Robinia pseudoacacia*	U74220.1	1470
Trifolium	*Trifolium repens*	EU677060	617
Ononis	*Ononis spinosa*	Z70174.1	1368
Euphorbia	*Euphorbia polychroma*	AY794827.1	1408
*Mespilus**	*Eriobotrya japoica*	U06800.1	1398
*Padellus**	*Prunus sargentii*	AF314014.1	1398
*Amygdalus**	*Prunus apetala*	AF411500.1	1398
*Ostrya**	*Ostryopsis davidiana*	AF081515.1	1428
*Pyracantha**	*Sorbus discolor*	GU363789.1	703
*Cydonia**	*Chaenomeles speciosa*	GU363806.1	703
Duschekia	*Alnus viridis*	FJ844588.1	1357
*Medicago**	*Genista germanica*	Z70098.1	1368
Teucrium	*Teucrium chamaedrys*	Z37465.1	1420
Origanum	*Origanum vulgare*	Z37427.1	1420
Lamium	*Lamium maculatum*	Z37402.1	1420
Stachys	*Stachys sylvatica*	Z37464.1	1420
Osmunda	*Osmunda regalis*	EF588706.1	1309

Table S3: Calibration points used in the phylogenetic tree predicted from records of scolytids in amber (Petrov and Perkovsky, 2008; Kirejtshuk, 2009 and Kirejtshuk et al., 2009).

Taxon	**Geological era**	**Age (Mio. years)**
Scolytinae	Lower Cretaceous	130
Cryphalus	Upper Eocene	37
Dryocoetes	Lower Oligocene	31
Tomicus	Upper Eocene	37
Taphrorhychus	Upper Eocene	37
Pityophthorus	Lower Miocene	20
Gnathotrichus	Lower Miocene	20
Ips	Upper Eocene	37
Hylastes	Upper Eocene	37
Hylurgops	Upper Eocene	37
Hylesinus	Lower Oligocene	31
Hylastinus	Upper Oligocene	37
Scolytus	Lower Miocene	20
Xylechinus	Upper Eocene	37
Xyleborus	Upper Eocene	37

Table S4: Host specificity measured as the root phylogenetic diversity index (Root PD) for 113 central European scolytids. The resource availability was obtained from the German National Forest Inventory (BWI2) of 2001 (www.bundeswaldinventur.de). The maximum numbers of yearly generations (Generation max.) are from Pfeffer (1994), the regions 0–18 in Germany are from Köhler and Klausnitzer (1998), and the pest scores 0–16 are from Grégoire and Evans (2004). An asterisk by the taxon name indicates an ambrosia feeder; taxons without an asterisk are phloem feeders.

Taxon	Root PD	Resource availability (basal area in m^2)	Host genera	Generation max.	Regions in Germany	Pest score
Carphoborus minimus (Fabricius,1798)	0.10	78,301,888	1	2	1	
Cryphalus abietis (Ratzeburg, 1837)	0.15	212,875,546	5	2	18	
Cryphalus intermedius Ferrari, 1867	0.11	86,720,539	2	2	1	
Cryphalus numidicus Eichhoff, 1878	0.13	84,733,216	3	2	0	
Cryphalus piceae (Ratzeburg, 1837)	0.11	120,849,358	2	2	13	3
Cryphalus saltuarius Weise, 1891	0.13	199,151,246	3	1	8	
Crypturgus cinereus (Herbst, 1793)	0.20	199,151,246	4	2	18	
Crypturgus hispidulus Thomson, 1870	0.15	207,569,897	4	2	14	
Crypturgus pusillus (Gyllenhal, 1813)	0.15	212,875,546	5	2	18	
Cyclorhipidion bodoanus (Reitter, 1913)*	0.18	27,679,224	2	1	6	
Dendroctonus micans (Kugelann, 1794)	0.11	192,719,918	2	1	17	3
Dryocoetes alni (Georg, 1856)	0.21	55,312,386	4	2	17	
Dryocoetes autographus (Ratzeburg, 1837)	0.15	207,569,897	4	2	18	
Dryocoetes hectographus Reitter, 1813	0.12	129,268,009	3	1	4	
Dryocoetes villosus (Fabricius, 1792)	0.18	27,679,224	2	2	18	
Ernoporicus caucasicus (Lindemann, 1876)	0.23	1,671,874	2	2	13	
Ernoporicus fagi (Fabricius, 1798)	0.20	53,387,370	2	2	18	
Ernoporus tiliae (Panzer, 1793)	0.23	5,579,165	2	2	14	
Gnathotrichus materiarius (Fitch, 1858)*	0.13	206,444,218	4	1	11	1
Hylastes angustatus (Herbst, 1793)	0.11	192,719,918	2	3	16	
Hylastes ater (Paykull, 1800)	0.10	78,301,888	1	2	18	
Hylastes attenuatus Erichson, 1836	0.10	78,301,888	1	2	17	
Hylastes brunneus Erichson, 1836	0.11	192,719,918	2	1	17	
Hylastes cunicularius Erichson, 1836	0.09	114,418,030	1	2	18	
Hylastes linearis Erichson, 1836	0.10	78,301,888	1	2	10	
Hylastes opacus Erichson, 1836	0.10	78,301,888	1	2	18	
Hylastinus obscurus (Marsham, 1802)	0.30	not available	6	1	14	
Hylesinus crenatus (Fabricius, 1787)	0.26	33,186,058	4	1	17	1
Hylesinus oleiperda (Fabricius, 1792)	0.18	5,757,261	3	1	15	
Hylurgops glabratus (Zetterstedt, 1828)	0.09	114,418,030	1	0	6	
Hylurgops palliatus (Gyllenhal, 1813)	0.15	207,56,9897	4	2	18	
Hylurgus ligniperda (Fabricius, 1787)	0.10	78,301,888	1	3	16	1
Ips acuminatus (Gyllenhal, 1827)	0.11	192,719,918	2	2	13	8
Ips amitinus (Eichhoff, 1871)	0.11	192,719,918	2	2	12	7
Ips cembrae (Heer, 1836)	0.13	201,138,569	3	2	17	5
Ips duplicatus (Sahlberg, 1836)	0.11	192,719,918	2	1	1	3
Ips sexdentatus (Börner, 1776)	0.11	192,719,918	2	4	17	6
Ips typographus (Linné, 1758)	0.13	199,151,246	3	3	18	16
Kissophagus hederae (Schmitt, 1843)	0.11	not available	1	1	11	
Leperisinus fraxini (Panzer, 1779)	0.25	33,162,005	4	1	18	3
Leperisinus orni (Fuchs, 1906)	0.17	5,757,261	1	1	7	

Lymantor aceris (Lindemann, 1875)	0.33	4,902,658	4	1	3	
Lymantor coryli (Perris, 1853)	0.23	4,290,078	3	1	16	
Orthotomicus erosus (Wollaston, 1857)	0.11	78,301,888	2	4	0	1
Orthotomicus laricis (Fabricius, 1792)	0.13	201,138,569	3	2	18	
Orthotomicus longicollis (Gyllenhal, 1827)	0.10	78,301,888	1	2	2	
Orthotomicus proximus (Eichhoff, 1867)	0.10	78,301,888	1	2	14	
Orthotomicus suturalis (Gyllenhal, 1827)	0.13	201,138,569	3	2	18	
Phloeophthorus rhododactylus (Marsham, 1802)	0.21	not available	5	1	17	
Phloeosinus aubei (Perris, 1855)	0.15	not available	5	2	8	
Phloeosinus thujae (Perris, 1855)	0.11	not available	3	2	16	
Phloeotribus caucasicus Reitter, 1891	0.17	5,757,261	1	1	2	
Phthorophloeus spinulosus Rey, 1883	0.09	114,418,030	1	1	8	
Pityogenes bidentatus (Herbst, 1784)	0.11	192,719,918	2	2	18	
Pityogenes bistridentatus (Eichhoff, 1878)	0.11	86,720,539	2	2	0	
Pityogenes chalcographus (Linné, 1761)	0.15	212,875,546	5	2	18	8
Pityogenes conjunctus (Reitter, 1887)	0.10	78,301,888	1	1	3	1
Pityogenes irkutensis Eggers, 1910	0.12	84,733,216	2	1	1	
Pityogenes quadridens (Hartig, 1834)	0.10	78,301,888	1	1	16	
Pityogenes trepanatus (Nördlinger, 1848)	0.10	78,301,888	1	2	12	
Pityokteines curvidens (Germar, 1824)	0.09	6,431,327	1	2	7	5
Pityokteines spinidens (Reitter, 1894)	0.09	6,431,327	1	2	3	3
Pityokteines vorontzowi (Jacobson, 1895)	0.09	6,431,327	1	2	4	3
Pityophthorus buyssoni Reitter, 1901	0.10	78,301,888	1	1	0	
Pityophthorus carniolicus Wichmann, 1910	0.10	78,301,888	1	1	2	
Pityophthorus exsculptus (Ratzeburg, 1837)	0.11	192,719,918	2	1	5	
Pityophthorus glabratus Eichhoff, 1878	0.10	78,301,888	1	1	15	
Pityophthorus henscheli Seitner, 1887	0.10	78,301,888	1	1	1	
Pityophthorus knoteki Reitter, 1898	0.10	78,301,888	1	1	1	
Pityophthorus lichtensteini (Ratzeburg, 1837)	0.11	192,719,918	2	2	17	
Pityophthorus micrographus (Linné, 1758)	0.15	207,569,897	4	2	1	
Pityophthorus pityographus (Ratzeburg, 1837)	0.19	212,875,546	6	2	15	3
Pityophthorus pubescens (Marsham, 1802)	0.10	78,301,888	1	1	14	
Polygraphus grandiclava Thomson, 1886)	0.31	193,872,017	3	1	13	
Polygraphus poligraphus (Linné, 1758)	0.11	192,719,918	2	2	18	5
Polygraphus subopacus Thomson, 1871	0.11	1927,19918	2	1	1	
Pteleobius kraatzi Eichhoff, 1864	0.18	365,584	1	1	4	
Pteleobius vittatus (Fabricius, 1787)	0.18	365,584	1	1	11	
Scolytus carpini (Ratzeburg, 1837)	0.23	80,809,318	5	2	14	
Scolytus ensifer Eichhoff, 1881	0.20	365,584	2	1	1	
Scolytus intricatus (Ratzeburg, 1837)	0.23	81,066,595	5	2	18	5
Scolytus kirschii Skalitzky, 1876	0.18	365,584	1	1	2	
Scolytus laevis Chapius, 1869	0.23	440,961	3	1	10	3
Scolytus mali (Bechstein, 1805)	0.30	2,657,464	13	2	18	
Scolytus multistriatus (Marsham, 1802)	0.18	365,584	1	2	18	8
Scolytus pygmaeus (Fabricius, 1787)	0.18	365,584	1	2	16	
Scolytus ratzeburgi Janson, 1856	0.17	9,584,764	1	1	15	1
Scolytus rugulosus (Müller, 1818)	0.49	3,143,589	17	2	18	
Scolytus scolytus (Fabricius, 1775)	0.20	365,584	2	2	17	9
Taphrorychus bicolor (Herbst, 1793)	0.23	86,972,801	4	2	18	
Taphrorychus villifrons (Dufour, 1843)	0.23	81,066,595	4	2	2	
Thamnurgus kaltenbachi (Bach, 1849)	0.25	not available	4	1	7	
Thamnurgus varipes Eichhoff, 1878	0.18	not available	1	1	1	
Tomicus minor (Hartig, 1834)	0.10	78,301,888	1	2	15	8
Tomicus piniperda (Linné, 1758)	0.10	78,301,888	1	2	18	9
Trypophloeus asperatus (Gyllenhal, 1813)	0.19	4,232,489	2	1	14	
Trypophloeus granulatus (Ratzeburg, 1837)	0.19	4,232,489	2	1	4	

Trypophloeus rybinskii Reitter, 1894	0.19	4,232,489	2	1	2	
Xyleborus alni Niijima, 1909*	0.27	44,493,688	5	1	8	
Xyleborus cryptographus (Ratzeburg, 1837)*	0.17	2,959,600	1	1	11	
Xyleborus dispar (Fabricius, 1792)*	0.68	191,153,643	16	1	18	2
Xyleborus dryographus (Ratzeburg, 1837)*	0.23	28,044,809	3	2	18	
Xyleborus eurygraphus (Ratzeburg, 1837)*	0.10	78,301,888	1	1	3	
Xyleborus germanus (Blandford, 1894)*	0.58	301,025,012	11	2	12	
Xyleborus monographus (Fabricius, 1792)*	0.25	77,159,305	4	1	17	
Xyleborus pfeili (Ratzeburg, 1837)*	0.17	6,180,686	1	1	3	
Xyleborus saxesenii (Ratzeburg, 1837)*	0.70	268,193,753	19	2	18	
Xylechinus pilosus (Ratzeburg, 1837)*	0.13	199,151,246	3	1	16	
Xylocleptes bispinus (Duftschmid, 1825)*	0.19	not available	1	1	16	
Xyloterus domesticus (Linné, 1758)*	0.40	101,484,278	8	1	18	3
Xyloterus laeve (Eggers, 1939)*	0.11	192,719,918	2	1	2	
Xyloterus lineatus (Olivier, 1795)*	0.16	207,569,897	5	1	18	3
Xyloterus signatus (Fabricius, 1787)*	0.37	50,609,028	5	1	17	1

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Borkenkäferzönosen in wärmegetönten Eichenmischwäldern Nordbayerns

Bark Beetle Communities in Oak-Mixed-Forests on Warm Stands in Northern Bavaria

Von Heinz Bussler und Jörg Müller

1 Einleitung

Im Jahr 2002 wurde im Rahmen eines Forschungsprojekts der Bayerischen Landesanstalt für Wald und Forstwirtschaft in Freising (LWF) die xylobionte Käferfauna wärmegetönter Eichenmischwälder in Nordbayern untersucht. 10 Probeflächen von je einem Hektar Fläche wurden im Bereich der Südlichen Fränkischen Platte und im benachbarten Vorderen Steigerwald ausgewählt, dabei wurden verschiedene Eichenmischwaldtypen wie Mittelwälder, Überführungswälder und Naturwaldreservate in das Projekt einbezogen. Durch einen breiten Methodenmix, der Handfang, Lichtfang, Baumkronenbenebelung sowie Flugeklektoreinsatz im bodennahen Stratum und im Kronenraum umfasste, konnte umfangreiches Material gewonnen werden.

2 Ergebnisse

Es wurden 322 xylobionte Käferarten in 15.175 Individuen nachgewiesen, darunter 29 Borkenkäferarten in 9.272 Exemplaren (Tab. 1). Die Scolytiden stellten 9 % der Arten, aber 61 % der Individuen und waren somit eindeutig die „Herren der Rinde" in den untersuchten Wäldern.

Das Artenspektrum wurde mit 21 Arten von „Laubholzborkenkäfern" dominiert, die vielen Mischbaumarten in den Eichenwäldern des Gebiets bereichern hierbei das Artenspektrum deutlich. Nicht autochthone Nadelhölzer waren in den Untersuchungsgebieten mit unter 2 % an der Bestockung beteiligt, gleichwohl fanden sich acht „Nadelholzarten" unter den Borkenkäfern. Diese dispergierten in 40 Exemplaren (0,4 %) in die Laubwaldflächen, wurden vor allem in den Flugeklektoren im Kronenraum nachgewiesen und sind als Influente zu werten. *Pityogenes trepanatus* und *Trypophloeus asperatus* sind gefährdete Arten der Roten Liste Deutschlands (Geiser 1998a), die „Zitterpappelart" *Trypophloeus asperatus* galt in Bayern als verschollen (Geiser 1998b) und konnte nach über 100 Jahren erstmals wieder nachgewiesen werden.

Abundanz und Dominanz

Fünf eudominante, dominante und subdominante (Dominanzklassifizierung nach Engelmann 1978) Arten stellten 91,4 % der Individuen, drei rezedente Arten 6,6 % und 21 subrezedente Arten die restlichen 2,0 %.

Tab. 1: **Nachgewiesene Borkenkäferarten.**

Taxon	Exempl.	(in %)	Dominanz	Brutbaumarten
Xyleborus dispar (F., 1792)	3032	(32,7)	eudominant	Polyphag in Laubhölzern
Xyleborus germanus (Blandf., 1894)	1976	(21,3)	dominant	Polyphag in Laubhölzern
Xyleborus peregrinus Eggers, 1944	1610	(17,3)	dominant	Eiche
Xyleborus saxeseni (Ratz., 1837)	1187	(12,8)	dominant	Polyphag in Laubhölzern
Xyloterus signatus (F., 1787)	666	(7,2)	subdominant	Eiche (div. Laubhölzer)
Scolytus intricatus (Ratz., 1837)	269	(2,9)	rezedent	Eiche
Dryocoetes villosus (F., 1792)	247	(2,7)	rezedent	Eiche
Leperisinus fraxini (Panz., 1799)	95	(1,0)	rezedent	Esche
Scolytus rugulosus (Müll., 1818)	8	(0,1)	subrezedent	Rosengewächse
Scolytus carpini (Ratz., 1837)	41	(0,4)	subrezedent	Hainbuche
Scolytus ratzeburgi Janson, 1856	1	(0,0)	subrezedent	Birke
Hylaster ater (Payk., 1800)	3	(0,0)	subrezedent	Kiefer
Hylurgops palliatus (Gyll., 1813)	7	(0,0)	subrezedent	Fichte (Kiefer)
Polygraphus poligraphus (L., 1758)	9	(0,1)	subrezedent	Fichte (Kiefer)
Hylesinus crenatus (F., 1787)	1	(0,0)	subrezedent	Esche
Hylesinus oleiperda (F., 1792)	4	(0,0)	subrezedent	Esche
Dryocoetus autographus (Ratz., 1837)	5	(0,1)	subrezedent	Fichte, Kiefer
Trypophloeus asperatus (Gyll., 1813)	1	(0,0)	subrezedent	Zitterpappel
Cryphalus abietis (Ratz., 1837)	1	(0,0)	subrezedent	Fichte, Kiefer
Ernoporicus fagi (F., 1778)	5	(0,1)	subrezedent	Rotbuche (Hainbuche)
Ernoporicus tiliae (Panz., 1793)	4	(0,0)	subrezedent	Winterlinde (Hainbuche)
Pityophthorus pityographus (Ratz., 1837)	4	(0,0)	subrezedent	Fichte (Kiefer)
Pityogenes chalcographus (L., 1761)	10	(0,1)	subrezedent	Fichte (Kiefer)
Pityogenes trepanatus (Nördl., 1848)	1	(0,0)	subrezedent	Kiefer
Taphrorychus bicolor (Hbst., 1793)	4	(0,0)	subrezedent	Rotbuche, Hainbuche
Xyleborus cryptographus (Ratz., 1837)	20	(0,2)	subrezedent	Zitterpappel
Xyleborus monographus (F., 1792)	37	(0,4)	subrezedent	Eiche
Xyleborus dryographus (Ratz., 1837)	2	(0,0)	subrezedent	Eiche
Xyloterus domesticus (L., 1758)	22	(0,2)	subrezedent	Polyphag in Laubhölzern
Summe	9272	(100,0)		

Eudominant waren der Ungleiche Holzbohrer (*Xyleborus dispar*) mit 32,7 % der Individuen. Im Gegensatz zum Obstbau war die Art unter Forstschutzaspekten bisher eher unbedeutend. Sie verursachte jedoch in jüngster Zeit in Bayern vermehrt Schäden an Ahornkulturen (FEEMERS 2003).

Dominant waren der Schwarze (Asiatische) Nutzholzborkenkäfer (*Xyleborus germanus*) mit 21,3 %, die Adventivart *Xyleborus peregrinus* mit 17,4 % und der Kleine Holzbohrer (*Xyleborus saxeseni*) mit 12,8 %. Mit einem Anteil von 7,2 % der Individuen war der Eichennutzholzborkenkäfer (*Xyloterus signatus*) nur subdominant vertreten.

Adventivarten

Xyleborus germanus wurde vermutlich aus Japan mit Eichenholz nach Deutschland eingeschleppt und wird seit 1952 bei uns nachgewiesen (SCHEDL 1981). RAULEDER berichtet 2003 über Erhebungen zum Flugverlauf von *Xyleborus dispar* und *Xyleborus saxeseni* als Schadarten in Obstbaumkulturen bei Karlsruhe. Er erwähnt hierbei auch Flugfallenfänge von Männchen des Ungleichen Holzbohrers in größerer Anzahl. Da dies nicht richtig sein konnte, weil die Männchen der Art flugunfähig sind, wurde eine Abbildung in der Publikation überprüft. Es zeigte sich, dass *Xyleborus germanus* fälschlicherweise für männliche *Xyleborus dispar* gehalten wurde. Dies bestätigte sich bei einer Nachbestimmung von sechs Belegexemplaren aus Karlsruhe durch die Bayerische Landesanstalt für Wald und Forstwirtschaft. Die verkannte Adventivart dürfte daher im Obstbau ein größere Rolle spielen als bisher bekannt ist.

Xyleborus peregrinus wurde erstmals für Deutschland von KÖHLER 1992 publiziert. Es handelt sich um eine Adventivart unbekannter Herkunft, die 1944 nach einem Einzelexemplar aus Stuttgart beschrieben wurde (peregrinus (griech.) „der Fremde") und danach in Vergessenheit geriet. Sie wurde wahrscheinlich im 20. Jahrhundert nach Deutschland importiert und breitet sich in jüngster Zeit rasch aus (KÖHLER 2000).

Die beiden Adventivarten stellten in der Untersuchung 38,7 % der Borkenkäferindividuen und sind somit dominant in den untersuchten Waldökosystemen etabliert. Die ökologischen Auswirkungen dieser Entwicklung sollten sorgfältig beobachtet werden.

Phänologie und Stratifikation ausgewählter Arten

Schwärmflugbeginn, -höhepunkt und -verlauf sind bei Borkenkäferarten arttypisch, variieren jedoch mit Regional- und Mikroklima und Jahreswitterungsverlauf (Abb. 1). Bekanntermaßen ist der Eichennutzholzborkenkäfer (*Xyloterus signatus*) ein „Frühschwärmer" (März, April) mit Maximum im Mai, der Eichensplintkäfer (*Scolytus intricatus*) dagegen ein Spätschwärmer mit Flugbeginn im Juni und Kulmination im Juli. Der Ungleiche Holzbohrer (*Xyleborus dispar*) erschien im Mai und hatte hier auch bereits sein Maximum, ab August wurde die Art nicht mehr nachgewiesen. Der Kleine Holzbohrer (*Xyleborus saxeseni*) flog bereits vereinzelt im April, kulminierte im Juni und hatte im September mit Ausflug der Jungkäfer nochmals eine kleine Aktivitätsspitze.

Die Adventivarten *Xyleborus germanus* und *Xyleborus peregrinus* sind als „Spätschwärmer" zu charakterisieren, sie flogen erstmals im Mai und erreichten ihre höchsten Abundanzen im Juni/Juli, wobei der Kulminationspunkt bei *Xyleborus peregrinus* ausgeprägt zweigipflig ist. Bei dieser Art konnte auch ein Ausflug von Jungkäfern im September bestätigt werden.

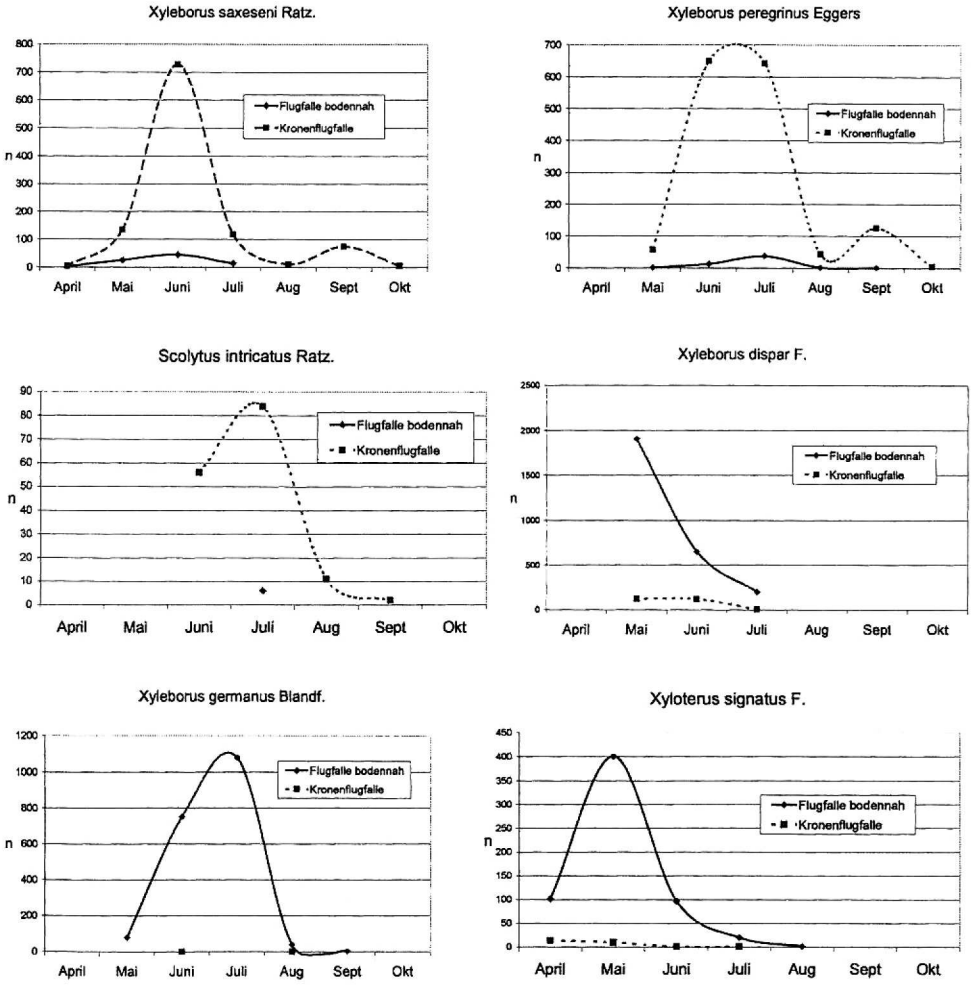

Abb. 1: Phänologie und Stratifikation ausgewählter Borkenkäferarten basierend auf Flugfallenfängen.

Sehr markant ist auch die Stratifikation der Arten, die aufgrund der unterschiedlichen Fangzahlen in den bodennahen Flugfallen und in den Kronenflugfallen dokumentiert werden konnte. Während *Xyloterus signatus*, *Xyleborus dispar* und *Xyleborus germanus* das bodennahe Stratum präferieren, sind *Scolytus intricatus*, *Xyleborus saxeseni* und *Xyleborus peregrinus* überwiegend Kronenraumbesiedler. Alle aufgeführten *Xyloterus*- und *Xyleborus*-Arten sind Holzbrüter (Ambrosiapilzzüchter), nur *Scolytus intricatus* ist ein Rindenbrüter. Die Adventivarten *Xyleborus germanus* und *Xyleborus peregrinus* besiedeln vertikal getrennte Straten.

Räuberische Antagonisten

Die gefährdeten Käferarten der Roten Liste Deutschlands (GEISER 1998a) *Aulonium trisulcum*, *Colydium elongatum* und *Corticeus bicolor* sind räuberische Antagonisten von Borkenkäferarten, die jedoch nur einzeln nachgewiesen wurden. Mit 86 Exemplaren wurde nur der Jagdkäfer (*Nemosoma elongatum*) in

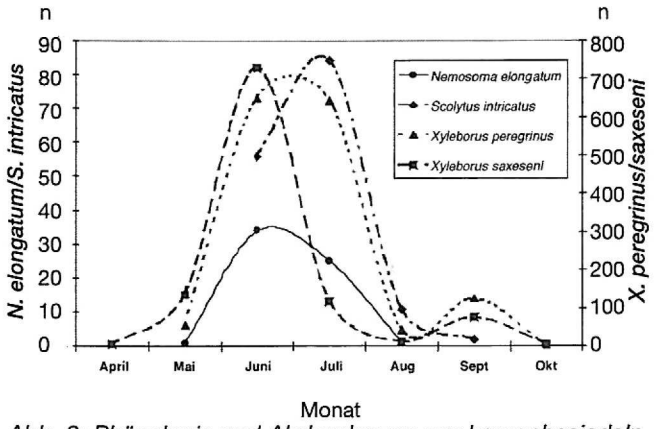

Abb. 2: Phänologie und Abdundanzen von kronenbesiedelnden Borkenkäferarten und ihrem Antagonisten Nemosoma elongatum L.

nennenswerten Mengen überwiegend in Kronenflugfallen festgestellt. Die Trogositiden-Art ist als polyphager Gegenspieler vieler Scolytidenarten bekannt (ESCHERICH 1923).

Das Aktivitätsmaximum der Imagines von *Nemosoma elongatum* deckt sich weitgehend mit dem Kulminationspunkt der Schwärmphase der Beutearten. Die Eiablage der Art erfolgt somit im Optimum des Nahrungsangebots, die Larven des Jagdkäfers ernähren sich danach von den verschiedenen Borkenkäferlarven. SKATULLA u. FEICHT (1992) konnten zeigen, dass dieser Räuber für Flugaktivitäten eine Temperatur über 19 °C benötigt.

Der Einfluss von Lichtigkeit und Nutzung auf Stratengilden von Borkenkäferarten

Auf eine Holznutzung mit einem künstlich erweiterten Brutsubstratangebot und daraus resultierender zunehmender Lichtigkeit der Bestände reagierten die Arten unterschiedlich (Abb. 3). *Xyleborus dispar* zeigte im Jahr 2002 einen deutlichen Dichteanstieg nach einer im Jahr 2000 erfolgten Holznutzung in den Mittelwaldflächen und nach frischen Hieben im Jahr 2001 in den Verjüngungsnutzungen des Überführungswaldes. *Xyloterus signatus* und *Xyleborus germanus* hingegen reagierten auf diese Hiebsmaßnahmen nicht, sie bevorzugen offensichtlich geschlossenere Bestände. Die ambrosiapilzzüchtenden Arten besitzen unterschiedliche Feuchtigkeitsansprüchen an ihr Brutsubstrat. Auf lichteren und besonnten Flächen ist diese in der Regel im Substrat geringer als in geschlossenen und schattigen Beständen.

Unter den Arten im Kronenraum reagierte *Xyleborus peregrinus* am deutlichsten auf Nutzung und Auflichtung

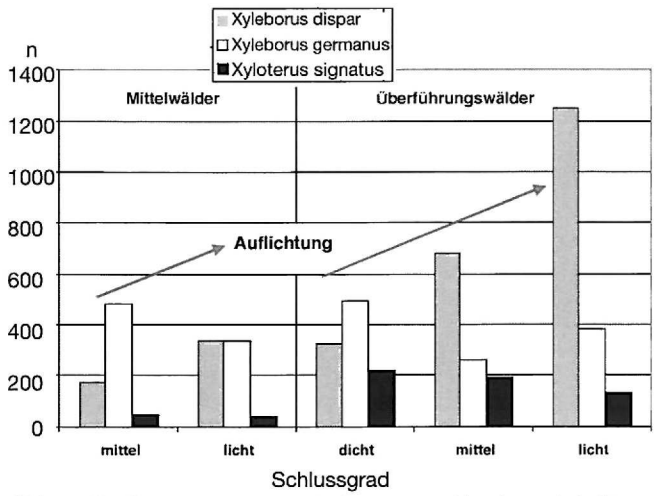

Abb. 3: Einfluss von Licht und Nutzung auf bodennah brütende Borkenkäferarten.

(Abb. 4). Eine abgeschwächte Reaktion zeigte auch der Eichensplintkäfer (*Scolytus intricatus*) auf einen frischen Hieb in der Hochwaldprobefläche, extrem gering waren seine Dichten dagegen in den geschlossenen Beständen des Naturwaldreservates und im dichten Überführungswald.

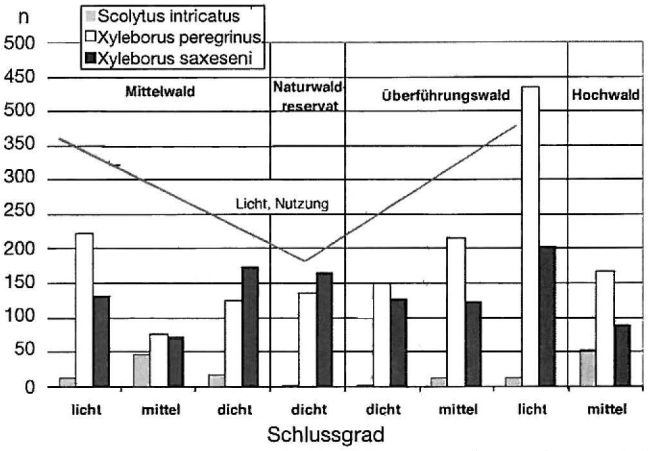

Abb. 4: Einfluss von Licht und Nutzung auf „kronenbrütende" Borkenkäferarten.

3 Zusammenfassung

Im Jahr 2002 wurde im Rahmen eines Forschungsprojekts der Bayerischen Landesanstalt für Wald und Forstwirtschaft in Freising (LWF) die xylobionte Käferfauna wärmegetönter Eichenmischwälder in Nordbayern mit einem breiten Methodenmix untersucht.

Es konnten 322 xylobionten Käferarten in 15.175 Individuen nachgewiesen werden, darunter 29 Borkenkäferarten in 9.272 Exemplaren. Die Scolytiden stellten 9 % der Arten, aber 61 % der Individuen und waren somit eindeutig die „Herren der Rinde" in den untersuchten Wäldern.

Eudominant waren der Ungleiche Holzbohrer (*Xyleborus dispar*) mit 32,7 % der Individuen, dominant der Schwarze (Asiatische) Nutzholzborkenkäfer (*Xyleborus germanus*) mit 21,3 %, die Adventivart *Xyleborus peregrinus* mit 17,4 % und der Kleine Holzbohrer (*Xyleborus saxeseni*) mit 12,8 %. Mit einem Anteil von 7,2 % der Individuen war der Eichennutzholzborkenkäfer (*Xyloterus signatus*) nur subdominant vertreten.

Die beiden Adventivarten *Xyleborus peregrinus*, dessen Herkunft unbekannt ist, und der aus Asien eingeschleppte *Xyleborus germanus* stellten in der Untersuchung 38,7 % der Borkenkäferindividuen und sind somit dominant in den Eichenwäldern des Untersuchungsgebietes etabliert. Welche Auswirkungen dies haben wird, bleibt abzuwarten. Als räuberischer Antagonist verschiedener Scolytiden im Kronenraum wurde nur der Jagdkäfer *Nemosoma elongatum* in bemerkenswerten Stückzahlen nachgewiesen. Die Phänologie, Stratifikation und der Einfluss von Lichtigkeit und Nutzung auf die Abundanzen ausgewählter Borkenkäferarten wird vorgestellt.

Abstract

In a scientific project in 2002 the "Bayerische Landesanstalt für Wald und Forstwirtschaft" (LWF) in Freising (Bavaria) surveyed the xylobiontic beetles of oak woods on warm stands of Northern Bavaria, using different sampling methods simultaneously.

The analysis of the samples revealed 15,175 specimens and 322 species of xylobiontic beetles, among them 29 species of bark beetles (*Scolytidae*) in 9,272 specimens. The Scolytids take 9 % of the total species number, but 61 % of all sampled specimens, which shows the dominance of this beetles group in the surveyed oak forests.

The dominant species among the bark beetles were *Xyleborus dispar* (32.7 % of all specimens), *Xyleborus germanus* (21.3 %), the immigrated species *Xyleborus peregrinus* (17.4 %) and *Xyleborus saxeseni* (12.8 %). The percentage of *Xyloterus signatus*, a species typical for oaks, was only 7.2 %. The two adventive species *Xyleborus peregrinus* (whose origin is unknown) and *Xyleborus germanus* (originating from Asia) showed a percentage of together 38.7 % and are evidently well established in the oak woods of Northern Bavaria. The ecological consequences of this development should be considered carefully in further studies.

The only relevant predator of the Scolytids in the canopy is *Nemosoma elongatum* L. (*Trogositidae*), which was found in considerable numbers in the canopy.

Based on quantitative analysis, the aspects of phenology and stratification of the bark beetle species and the effects of different forest structure and management on the species composition are discussed.

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FDK: 453

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Artikel V

Neue Borkenkäferarten in Bayern – Eine Gefahr für Laub- und Nadelbäume

New bark beetle species in Bavaria – danger to deciduous and coniferous trees

Dipl. Forsting. Heinz Bussler

Zusammenfassung

Bisher wurden eingeschleppte Borkenkäferarten im Hinblick auf den Wald- und Waldnaturschutz und für sonstige Baumbestände eher als unproblematisch angesehen. Am Beispiel der Adventivarten (lat. advenire – hinzukommen) Amerikanischer Nutzholzborkenkäfer (*Gnathotrichus materiarius* FITCH), Bodemeyers Nutzholzborkenkäfer (*Cyclorhipidion bodoanus* RTT.), Japanischer Nutzholzborkenkäfer (*Xyleborus alni* NIISIMA), Schwarzer Nutzholzborkenkäfer (*Xyleborus germanus* BLANDF.) und des erstmals in Bayern nachgewiesenen Kleinen Eichenborkenkäfers (*Taphrorychus villifrons* DUF.) wird aufgezeigt, dass diese Arten jedoch ein erhebliches Gefährdungspotential für heimische Baumarten darstellen, dessen vollständige Auswirkungen nach derzeitigem Kenntnisstand nicht abschätzbar sind. *Xyleborus germanus* wird hierbei momentan als bedrohlichste Art betrachtet, er ist in Laubwäldern Nordbayerns schon die dominante Borkenkäferart und dringt zunehmend auch ins Offenland vor.

Summary

In respect to forest- and forest-nature conservation, introduced bark-beetle species were previously regarded as rather unproblematic. Considering the adventitious species *Gnathotrichus materiarius* FITCH, *Cyclorhipidion bodoanus* RTT., *Xyleborus alni* NIISIMA, *Xyleborus germanus* BLANDF. and *Taphrorychus villifrons* DUF. (this species being recorded for the first time in Bavaria) as examples, it is pointed out that these species do represent a substantial hazard potential for domestic tree species. At present, the entire effects are not assessable. *Xyleborus germanus* is momentarily regarded as the most dangerous species. In deciduous forests of northern Bavaria it is already the most dominant bark-beetle species and also penetrates increasingly into the open landscape.

1. Die Globalisierung der Fauna

Australische Bockkäfer sind in Spanien und Italien eingebürgert, eine indische Art in Großbritannien, nordamerikanische Spezies in Dresden und am Mittelmeer. Der Chinesische Laubholzbock (*Anoplophora chinensis* FORST.) ist auf dem Vormarsch in Italien und der Asiatische Laubholzbock (*Anoplophora glabripennis* MOTSCH.) steht in Österreich und Deutschland kurz vor seiner Etablierung. Bockkäfer sind groß, oft bunt und spektakulär. Deshalb genießen sie in den Medien eine hohe Aufmerksamkeit. Im Zuge des Welthandels, und durch die Globalisierung verstärkt, wurde aber auch eine wesentlich größere Anzahl kleiner und unscheinbarer Arten verschleppt. Diese bedrohliche Entwicklung bleibt außerhalb von Fachkreisen meist unbeachtet. Besonders verschiedene Borkenkäferarten bedürfen einer wesentlich stärkeren Aufmerksamkeit, da die Auswirkungen ihrer Einschleppung für die heimischen Baumarten überhaupt noch nicht abgeschätzt werden können.

2. Der Amerikanische Nutzholzbockkäfer – Der Neubürger aus der Nearktis

Der Amerikanische Nutzholzborkenkäfer (*Gnathotrichus materiarius* FITCH) stammt aus dem östlichen Teil Nordamerikas und ist dort von Ontario bis Florida verbreitet. Er tritt als technischer Holzschädling an verschiedenen Nadelbaumarten wie *Pinus*, *Picea*, *Abies*, *Larix*, *Tsuga* und *Pseudotsuga* auf (KAMP 1970). 1933 wurde diese Borkenkäferart in Europa zuerst in Nordwestfrankreich gefunden. Nachweise gelangen dann 1965 in Holland und fast zeitgleich in Deutschland im Schwarzwald (SCHEDL 1966). Wie die bisherigen Befunde aus Mitteleuropa zeigen, bevorzugt der Käfer bei uns als Brutbaum die Kiefer, Befall von Douglasie ist jedoch mehrfach belegt. Dies ist nicht weiter verwunderlich, da sich das ursprüngliche Herkunftsgebiet der Art mit dem der Douglasie in Nordamerika überschneidet. Es handelt sich um eine monogame holzbrütende und pilzzüchtende Borkenkäferart (SCHMIDT 2004). Alle Nutzholzborkenkäfer züchten in ihren Bohrgängen Ambrosiapilze, die den Larven als Nahrung dienen. Diese Pilze werden in speziellen Strukturen des Außenskeletts, den Mycetangien, gezielt zu neuen Brutbäumen transportiert (SCHAWALLER et al. 2005). Mit neuen Nutzholzborkenkäferarten werden deshalb auch ökosystemfremde Pilzarten verschleppt. Der Amerikanische Nutzholzborkenkäfer befindet sich noch immer in Ausbreitung. Nachweise liegen inzwischen aus Bayern, Baden-Württemberg, Hessen, Rheinland-Pfalz, Nordrhein-Westfalen, Hannover und dem Niederelbegebiet vor. Die Art ist aufgrund ihrer Herkunft sehr kälteresistent und wurde in Bayern bei der Anlage von Brutsystemen bereits im Januar beobachtet.

3. Xyleborus peregrinus – Der „Fremde", eine nicht erkannte sibirisch-nordasiatische Art

Der ebenfalls zu den Ambrosiakäfern gehörige *Xyleborus peregrinus* wurde 1944 von EGGERS nach einem bei Stuttgart gefundenen Weibchen beschrieben. „Peregrinus" heißt übersetzt der Fremde, da für EGGERS die Herkunft der Art ungeklärt war. Andererseits vermutete er aber, dass es sich um eine bisher übersehene heimische Art handeln könnte. *Xyleborus peregrinus* sollte laut Erstbeschreiber und verschiedenen Autoren *Xyleborus saxeseni* (RATZ., 1837) ähnlich sehen und wurde lange Zeit nicht von diesem getrennt. Die Art wurde erst 1992 aus Nordrhein-Westfalen wieder für Deutschland gemeldet. Erste Nachweise aus Baden-Württemberg aus dem Jahr 1979 erfolgten durch nachträgliche Bestimmung. Seit 1990 liegen viele Meldungen aus Bayern, Baden-Württemberg, Hessen, der Pfalz und vom Nordrhein vor. Nach Untersuchungen der Bayerischen Landesanstalt für Wald und Forstwirtschaft (LWF) in den Jahren 2002 und 2004 im Steigerwald und 2003 im Spessart ist „*Xyleborus peregrinus*" inzwischen eine teilweise dominante Borkenkäferart in den Laubwäldern Nordbayerns (BUSSLER & MÜLLER 2004).

Bei einer Überprüfung des Holotypus von *Xyleborus peregrinus* EGGERS, 1944 stellte sich nun heraus, dass es sich um ein etwas abweichendes Exemplar von *Xyleborus saxeseni* (RATZ., 1837) handelt. Alle aus Deutschland, Österreich, Schweiz und Frankreich gemeldeten *Xyleborus peregrinus* sind *Cyclorhipidion (Xyleborus) bodoanus*. Diese Art wurde von BODEMEYER anlässlich der Sibirien-Amur Exkursion gesammelt und von REITTER zu Ehren von BODO VON BODEMEYER 1913 beschrieben.

Es handelt sich also um eine sibirisch-nordasiatische Art, die taxonomisch korrekt *Cyclorhipidion bodoanus* (RTT., 1913), *syn. Xyleborus punctulatus* KURENZOV 1948, heißen muss. Über die Verbreitung der Art im Ursprungsgebiet und in Europa liegen keine umfassenden Angaben vor. Wann genau die Einschleppung nach Mitteleuropa erfolgte, ist ebenfalls ungeklärt. Die ersten Belege stammen nach den bisher vorliegenden Daten aus dem Jahr 1960 aus dem Elsaß. Die Entwicklung der Art erfolgt in Stämmen und starken Ästen von Eichen (*Quercus* spp.), selten von Esskastanie (*Castanea sativa*). Außerhalb von Waldbeständen konnte die Art 2005 bei Bernried am Starnberger See in lichten, mit Stieleichen bestockten Parkbereichen, nachgewiesen werden. *Cyclorhipidion bodoanus* entwickelt sich bevorzugt im Kronenstratum (BUSSLER & MÜLLER 2004), eine Beteiligung an der Komplexerkrankung von Eichen ist nicht auszuschließen.

4. Der Kleine Eichenborkenkäfer – Immigrant oder nur verkannt?

Der Kleine Eichenborkenkäfer (*Taphrorychus villifrons* DUF., 1843) wurde im Jahr 2005 erstmals in Bayern nachgewiesen. Im Gegensatz zu den anderen hier vorgestellten Arten handelt es sich um eine rindenbrütende Art. Im Rahmen eines Projekts der Bayerischen Landesanstalt für Wald und Forstwirtschaft (LWF) konnten in Unterfranken bei Werneck/Rundelshausen sieben Exemplare in Lichtfallen gefangen werden. Aus Deutschland sind bisher insgesamt nur sechs verstreute Fundorte der Art bekannt geworden (GEBHARDT 2003, KAMP 1983). Da es sich überwiegend um Wärmestandorte handelt, ist davon auszugehen, dass es sich bei diesem „Neubürger" nicht um eine eingeschleppte Art handelt, sondern dass der Käfer schon immer an geeigneten Standorten in kleinen Populationen vorhanden war, aber wegen seiner großen makroskopischen Ähnlichkeit mit dem Kleinen Buchenborkenkäfer (*Taphrorychus bicolor* HBST., 1793) bisher nicht erkannt wurde. Es ist anzunehmen, dass die Art begünstigt durch die Klimaerwärmung inzwischen in höheren Populationen auftritt und deshalb zukünftig häufiger nachgewiesen wird.

Der Kleine Eichenborkenkäfer (*Taphrorychus villifrons* DUF., 1843) wurde 1972 erstmals in Deutschland im „Mooswald bei Freiburg i. Br." gefunden, aber erst 1982 als neue Art für Deutschland erkannt (KAMP 1983). Von 2000 bis 2003 konnte die Art an fünf weiteren Fundorten in Baden und Württemberg, der Pfalz und in Westfalen nachgewiesen werden. Aus anderen Bundesländern waren bislang keine Funde der Art bekannt (GEBHARDT 2003). Der Kleine Eichenborkenkäfer ist eine südeuropäische Art, deren Verbreitungsschwerpunkt rund um das Mittelmeer liegt, und die von Südosten über die Slowakei und Ungarn bis nach Österreich einstrahlt. Besiedelt wird ein breites Wirtsbaumspektrum (*Quercus* spp., *Fagus orientalis*, *Carpinus* spp., *Castanea sativa*). In Deutschland wurde die Art bisher ausschließlich an *Quercus robur* festgestellt (GEBHARDT 2003). Der durch die Klimaerwärmung verursachte abiotische Stress für die heimischen Baumarten könnte durch die Zunahme und Ausbreitung von bisher nur reliktär und in kleinen Populationen vorkommenden Arten deutlich erhöht werden.

5. Der Japanische Nutzholzborkenkäfer – nicht nur eine Gefahr für Erlen

Der 1909 aus Japan beschriebene *Xyleborus alni* (NIISIMA) wurde 1991 erstmals in Niedersachsen für Deutschland gemeldet. Bereits 1988 wurde er im östlichen Mitteleuropa nachgewiesen. In den letzten Jahren folgten Meldungen aus weiteren Bundesländern. Wie viele andere pilzzüchtende Holzbrüter besiedelt *Xyleborus alni* ein weites Spektrum an Wirtsbäumen. Die Überwinterung der Imagines erfolgt im Brutgangsystem. Das Ausschwärmen der befruchteten Weibchen beginnt bereits während der ersten warmen Frühlingstage (GEBHARDT 2002). Die Männchen der Gattung *Xyleborus* verlassen die Bohrgänge dagegen kaum, sie sind flugunfähig und schlüpfen nur in geringer Zahl. Die Unterscheidung vom heimischen Kleinen Holzbohrer (*Xyleborus saxeseni*) ist nur Spezialisten möglich. Der bayerische Erstfund erfolgte 1998 bei Zuchering in gefällten Zitterpappeln (WEICHSELBAUMER 2003). 2001 wurde die Art am Rande des Forstenrieder Parks im Landkreis Starnberg an gelagertem Erlenholz gefunden. 2005 ebenfalls an Erlenlagerholz im Naturwaldreservat Tiroler Achen am Chiemsee (BUSSLER 2005). Weitere Bruthölzer, die befallen werden, sind Weiden, Stieleichen, Birken und sogar Hasel (PFEFFER 1994). In Hessen ist die Art inzwischen auch an Rotbuchen nachgewiesen. Man stellt sich hier die Frage, ob die Schadwirkungen an Buchen, die bisher anderen Borkenkäferarten zugeschrieben wurden, nicht durch die Adventivart *Xyleborus alni* verursacht werden (FLECHTNER 2004).

6. Der Schwarze Nutzholzborkenkäfer – ein Alleskönner

Ursprünglich stammt der Schwarze Nutzholzborkenkäfer (*Xyleborus germanus* BLANDF.) aus Ostasien. Er wurde in den 30er Jahren in die USA verschleppt und 1952 erstmals für Europa in Deutschland im Raum Darmstadt nachgewiesen (GROSCHKE 1953). Die Art hat sich auch in Frankreich, Belgien, Schweiz und Österreich stark ausgebreitet und wurde in Deutschland inzwischen in vielen Regionen nachgewiesen. Der Schwarze Nutzholzborkenkäfer erreicht eine Größe von 2 bis 2,3 mm und ist damit deutlich klei-

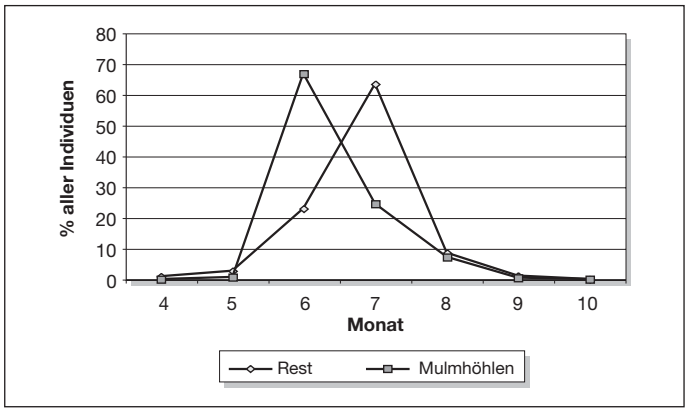

Abbildung 1:
Phänologie von *Xyleborus germanus* BLANDF. im Buchenwald. Er erreicht sein Aktivitätsmaximum an hohlen Bäumen bereits im Juni, dies könnte durch ein ausgeglicheneres Mikroklima in den Mulmhöhlen verursacht sein. An sonstigen Bäumen (Rest) liegt der Höhepunkt der Schwärmphase erst im Juli.

ner als der heimische *Xyleborus dispar* (F.), mit dem die Art gelegentlich verwechselt wird (RAULEDER 2004). Der Ambrosiapilzzüchter befällt sowohl Laub-, wie auch Nadelholz (ZACH et al. 2001). Er fliegt erstmals Ende April, erreicht seine höchsten Dichten aber erst im Juni und Juli (Abbildung 1).

Der Schwarze Nutzholzborkenkäfer bevorzugt die bodennahe Schicht der Wälder in der Höhenzone von null bis fünf Metern (Abbildung 2). Gleichfalls ist erkenntlich, dass Biotopbäume, also lebende Bäume mit Astabbrüchen, Spalten, Verpilzungen und Höhlen bevorzugt angeflogen werden. Bisher galt die Art als typischer Sekundärschädling. Jedoch wurde bereits an Laubholzheistern auch Primärbefall festgestellt. Das massive Auftreten an Biotopbäumen lässt zudem befürchten, dass der Käfer die für den Waldnaturschutz wertvollen Biotopbäume nachhaltig schädigt und zu einem beschleunigtem Absterben dieser Bäume beitragen kann. Sicherlich ist die Art der Wegbereiter für Nachfolgeschäden durch Braun- und Weißfäulepilze.

Der Schwarze Nutzholzborkenkäfer besitzt hinsichtlich Brutsubstratwahl (Baumarten, Stärke, Zersetzungsgrad) eine außergewöhnlich breite Valenz. Sowohl Laubholzheister, Holzerntestöcke, frisches und älteres Lagerholz, als auch anbrüchige stehende Bäume werden befallen. Wie Untersuchungen der LWF im Steigerwald zeigten, werden Bäume mit Verpilzungen und Mulmhöhlen deutlich bevorzugt (Abbildung 3). Mulmhöhlenbäume sind die exklusivsten Strukturen

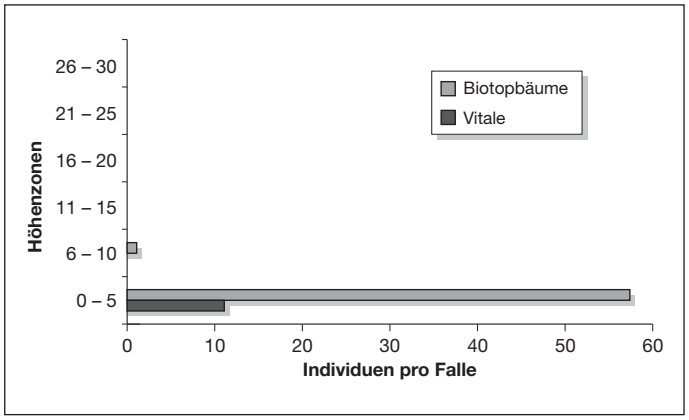

Abbildung 2:
Höhenstratifikation von *Xyleborus germanus* BLANDF. im Buchenwald. Durchschnittliche Fangzahlen pro Flugfensterfalle, getrennt nach vitalen Bäumen und Biotopbäumen.

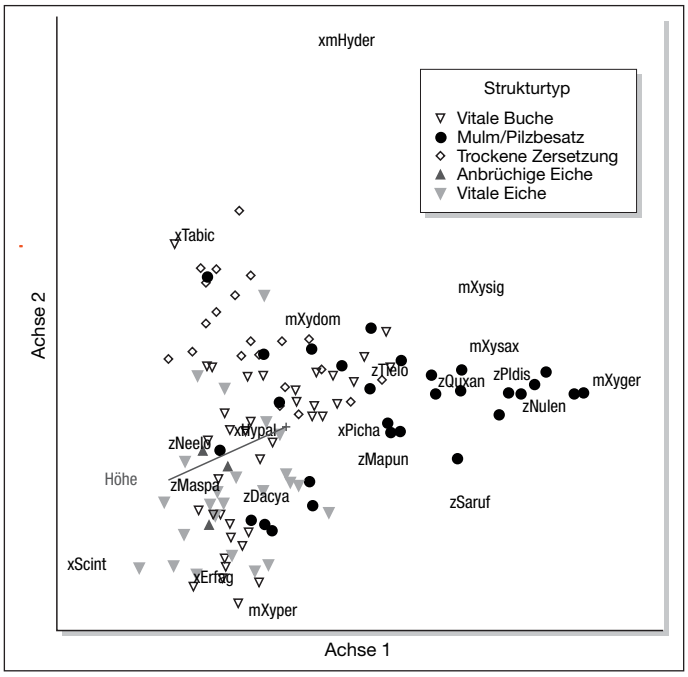

Abbildung 3: Vergesellschaftung und ökologische Einnischung von *Xyleborus germanus* im Buchenwald. Die DCA zeigt die Gruppierung von *Xyloborus germanus* BLANF. (mXyger) zu einer Gemeinschaft, die bodennahe Bereiche, Mulmhöhlenbäume und Bäume mit Verpilzungen bevorzugt.

in unseren Wäldern und Habitat für eine hochgradig gefährdete Lebensgemeinschaft. *Xyleborus germanus* befällt die Mulmhöhlenbäume in der Höhlung. Durch die Anlage seiner Brutsysteme im Inneren der Höhlenwände ermöglicht er es Fäulepilzen in das bisher nicht infizierte Splintholz vorzudringen. Dadurch wird die Zersetzung wesentlich beschleunigt und die Lebenserwartung der Bäume verringert.

Bisher wurden eingeschleppte Borkenkäferarten aus Sicht des Forstschutzes und des Waldnaturschutzes eher als unproblematisch angesehen. Aber die vorliegenden Befunde und die rasante Ausbreitung des Schwarzen Nutzholzborkenkäfers sind höchst problematisch. Auch die in Belgien vermutete Höhengrenze von maximal 350 Metern ü. NN für eine dauerhafte Ansiedlung der Art (HENIN & VERSTEIRT 2004) hat sich nicht bestätigt. Im Steigerwald und im Spessart wurde der Käfer auch in Höhenlagen zwischen 400 und 500 Metern festgestellt. Ein bisher nur ansatzweise diskutierter Effekt des Eindringens dieser Adventivart ist die Verdrängung von heimischen Arten. Bei Untersuchungen in Eichenmittelwäldern im Vorderen Steigerwald (BUSSLER & MÜLLER 2004) war der heimische *Xyleborus dispar* die absolut häufigste Art und *Xyleborus germanus* „nur" die zweithäufigste Art (3032 Ex.: 1976 Ex.). In den Buchenwäldern des nördlichen Steigerwaldes hingegen war *Xyleborus germanus* die dominante Art und *Xyleborus dispar* nur noch in wenigen Exemplaren vorhanden (1852 Ex.: 27 Ex.). Die invasive Art wird auch zunehmend im Offenland festgestellt, selbst an Weinreben (BÖLL 2005) und im Obstbau (RAUHLEDER 2004) wurde der Schwarze Nutzholzborkenkäfer in Deutschland inzwischen nachgewiesen.

7. Ausblick

Nicht die Einschleppung großer und spektakulärer Arten stellt für unsere Wald- und Baumbestände die Hauptgefahr dar, sondern die zunehmende Dominanz von kleinen und unscheinbaren Neozoen*. Bei Schä-

* Neozoen sind Tierarten, die definitionsgemäß nach dem Jahr 1492 unter direkter oder indirekter Mitwirkung des Menschen in ein bestimmtes Gebiet gelangt sind und dort wild leben (zur Zeit 1.322 Neozoenarten in Deutschland)

digungen von Bäumen durch holzbewohnende Insekten sollten deshalb nicht nur die „üblichen Verdächtigen“ in Betracht gezogen werden. Entscheidend für die Abschätzung des Gefährdungspotentials und für eventuelle Gegenmaßnahmen ist die exakte Bestimmung der Schadorganismen.

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Artikel VI

Remarks on the taxonomy, distribution and ecology of *Trypodendron laeve* EGGERS, 1939

(Coleoptera: Scolytidae)

Heinz BUßLER & Olaf SCHMIDT

Abstract

Resulting from the unclarified status and faulty synonymy of several species of the genus *Trypodendron*, the existence of a further ambrosia beetle in Europe has been widely ignored or overlooked in many studies on forest entomology. *Trypodendron laeve* EGGERS was first found in Austria in 1982. Several further records connected with imported conifer wood from Russia led to the view that the species is introduced to Central Europe and not native here. Records from the Bavarian Alps, the Bavarian Forest National Park and the Sumava National Park now suggest that this is a widely distributed and native, but mostly unrecognized boreo-montane species.

Introduction

Not even the correct name of the genus seems clear: *Trypodendron* STEPHENS, 1830, and *Xyloterus* ERICHSON, 1836, are both used as valid in current literature. *Trypodendron laeve* EGGERS, 1939, was described from Japan and *T. piceum* STRAND, 1946, from Norway (STRAND 1946). MARTIKAINEN 2000 considered *T. laeve* and *T. piceum* to be junior synonyms of *T. proximum* NIIJIMA, 1909, already described from Japan. EHNSTRÖM & AXELSSON 2002 list *T. proximum* as a member of the Swedish fauna. According to KNIZEK (pers. comm. 2008), *T. laeve* and *T. proximum* are however separate, valid species. This opinion was also expressed by KREHAN & HOLZSCHUH 1999, MANDELSHTAM & POPOVICHEV 1999 and ZELENY & DOLEZAL 2004. In the identification handbook for European bark beetles (GRÜNE 1979), neither *T. laeve* nor *T. piceum* is mentioned. In FREUDE, HARDE & LOHSE, the standard work for the identification of Central European beetles, SCHEDL 1981 places *T. laeve* and *T. piceum* as synonyms of *Xyloterus lineatus* (OLIVIER, 1795). This was first corrected in the supplementary volume of 1994, where *Xyloterus laeve* is treated as a valid species with *T. piceum* as its synonym (PFEFFER 1994). This confusion has led to a lack of awareness in many studies in forest entomology of the existence of a further species of ambrosia beetle in Europe (MARTIKAINEN 2000).

World distribution and records from Central Europe

According to KNIZEK (pers. comm. 2008) *Trypodendron proximum* occurs only in the East Palaearctic, not in Europe. Distribution of *Xyloterus laeve* is given by PFEFFER 1995 as Japan, Norway, Sweden and Lower Austria. According to HOLZSCHUH 1995 & 1999 and KREHAN & HOLZSCHUH 1999 the species is also known from Russia, China, Poland, Finland, Estonia and the Czech Republic. MARTIKAINEN (pers. comm. 2008) states that the specimens recorded by MARTIKAINEN 2000 as *Tryodendron proximum* from Finland are actually *T. laeve*. The species was first reported in Finland in 1990 (MUONA 1990), but according to MARTIKAINEN 2000 is widely distributed and abundant there and considered to be native. *T. laeve* was first discovered in Austria in 1982 in the federal state of Lower Austria and shortly thereafter in Burgenland (HOLZSCHUH 1990a), Upper Austria and Styria (HOLZSCHUH 1990b, KREHAN & HOLZSCHUH 1999). HOLZSCHUH 1990a/b & 1995 regards *T. laeve* as a forest pest which has been introduced to Austria. This is based on the fact that

records were concentrated around storage and handling yards containing conifer timber imported from East Europe.

In Germany *Xyloterus laevae* (sic!) is only recorded from Bavaria (KÖHLER & KLAUSNITZER 1998). The first German record is from 1953 in the Allgäu Region (leg. HANSEN, "Oberstdorf"?). This specimen has been traced and its identity confirmed (pers. comm. BÖHME 2008). In May-August 2007 ten specimens of *T. laeve* (2♂♂ and 8♀♀, leg. MÜLLER, det. BUßLER & BÜCHE, vid. KNIZEK) were sampled with flight interception traps near ground level, run as part of the biodiversity and climate project of the Bavarian Forest National Park **(Tab. 1)**. It is perhaps significant, that the first record of this species in the Bavarian Forest resulted from research on biodiversity and that *T. laeve* was not detected in any of the numerous previous investigations on forest entomology. *T. laeve* is also present in the neighbouring Sumava National Park, where ZELENY & DOLEZAL 2004 even suggest that it is a species of significance for nature conservation.

Tab. 1: Records of *Trypodendron laeve* in 2007 in the Bavarian Forest National Park

Geographic coordinates	month	specimens	a.s.l. (m)
X: 4593446 Y: 5441326	May	2	1150
X: 4600979 Y: 5424642	July	2	916
X: 4600979 Y: 5424642	Juni	1	916
X: 4601091 Y: 5425026	July	1	959
X: 4601175 Y: 5425314	July	2	989
X: 4601818 Y: 5427522	August	1	1352
X: 4603000 Y: 5421368	July	1	782

Identification, biology and ecology

Tryopdendron laeve is immediately distinguishable by its extensively blackened legs, which are always pale in *T. lineatum*. The morphology of *T. laeve* is however more similar to *T. signatum* (FABRICIUS, 1787) than to *T. lineatum*. Conspicuous is the sexually dimorphic structure of the antennal club in *T. laeve*. In the male this is inverted egg-shaped and resembles the club of *T. signatum*; in the female it is nearly spherical, as in *T. lineatum*. Further characters for separating *T. laeve* and *T. lineatum*, including a comparison of the male genitalia, are presented in full by HOLZSCHUH 1990a.

The following tree species have been recorded as hosts of *T. laeve*: *Picea* (HOLZSCHUH 1995), *Picea abies* (STRAND 1946), *Picea jeozoensis*, *Picea obovata*, *Picea abies* and *Pinus sylvestris* (PFEFFER 1994, 1995), *Picea abies* and *Pinus sylvestris* (MARTIKAINEN 2000). The appearance of galleries made by the brood of the conifer ambrosia beetles *T. laeve* and *T. lineatum*, with radial "ladder-rung" passages, is very similar. *T. laeve* appears very early in the year, and compared to *T. lineatum* apparently has only a short period of peak adult activity. In 1999 the flight period of the species in Austria ended as early as the last week of April (KREHAN & HOLZSCHUH 1999). The

specimens recorded from the Bavarian Forest National Park in July and August are probably young beetles which were searching for places to overwinter. According to studies in Finland, flight activity begins at temperatures as low as 13°C and reaches its peak at 15°C, which is the threshold for start of flight activity in *T. lineatum*. The flight periods of these two species hardly overlap. *T. laeve* appears to overwinter mainly under the bark of standing trees, or standing dead wood, which enables it to become active even when a closed covering of snow is present (MARTIKAINEN 2000). This may represent an important competitive advantage to *T. laeve* over *T. lineatum*, because closed coverings of snow often lie until late in May in the montane zone.

Discussion

Trypodendron laeve was first found in Austria in 1982 near Gahns at an altitude of 1300 m above sea level, and thereafter several times at timber yards, which caused it to be regarded as an introduced species (HOLZSCHUH 1990a/b & 1995, KREHAN & HOLZSCHUH 1999). The first record in Bavaria and at the same time first record for Central Europe is however from 1953 in the Allgäu. The most recent records in the Bavarian Forest and Sumava National Parks prompt us to question whether *T. laeve* might in fact be a native, boreomontane, relict species, which in most studies on forest entomology has been either ignored or overlooked, and so remained practically unrecorded until recently. Localities for the species in the Bavarian Forest National Park were between 782 and 1352 m a.s.l. A significant indication that the species may be indigenous, is that it is there found together with other, partly extremely rare, boreomontane faunal elements, e.g. *Bius thoracicus* F., *Corticaria interstitialis* MANNH., *Corticaria obsoleta* STRAND (REIKE & LIEPOLD 2004), *Orthocis pseudolinearis* LOHSE, *Xestobium austriacum* RTT., *Dryocoetes hectographus* RTT., *Anastrangalia reyi* HEYDEN or *Judolia sexmaculata* L. Above all, the occurrence of two *Corticaria* species in the Bavarian forest which were described from Swedish and Finnish Lapland, shows that eurytopic northern or mainly Fennoscandian species are also present in the Bavarian Forest.

Commencing in spring 2008, the distribution and abundance of *T. laeve* in the Bavarian Forest National Park will be studied more thoroughly, using pheromone traps. It will still however be necessary to search for this species in Germany in the Alps and in other, lower ranges of mountain.

Acknowledgments

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Zusammenfassung

Auf Grund des ungeklärten taxonomischen Status verschiedener Arten der Gattung *Trypodendron* und fehlerhafter Synonymisierung wurde die Existenz einer weiteren Nutzholzborkenkäferart in Europa in vielen forstentomologischen Untersuchungen bisher weitgehend ignoriert. *Trypodendron laeve* EGGERS wurde in Österreich erstmals 1982 gefunden. Mehrere weitere Nachweise im Zusammenhang mit importiertem Nadelholz aus Russland führten bisher zu der Ansicht, dass die Art nach Mitteleuropa eingeschleppt wurde und hier nicht heimisch ist. Funde aus dem Jahr 1953 im Allgäu, 2007 im Nationalpark Bayerischer Wald und aus dem Sumava Nationalpark im angrenzenden Tschechien lassen jedoch vermuten, dass es sich um eine verbreitete und autochthone, aber bisher weitgehend verkannte, boreomontane Art handelt. Felddiagnostisch ist *Tryopdendron laeve* durch seine meist umfangreich geschwärzten Beine von *Trypodendron lineatum*, mit immer hellen Beinen,

unterscheidbar. Weitere Unterscheidungskriterien zwischen *T. laeve* und *T. lineatum*, inklusive einem Vergleich der männlichen Genitalstrukturen, werden bei HOLZSCHUH 1990a ausführlich dargestellt. *T. laeve* brütet in Europa in Fichte (*Picea abies*) und Kiefer (*Pinus sylvestris*). Die Art erscheint sehr früh im Jahr, hat aber im Unterschied zu *T. lineatum* anscheinend nur eine sehr kurze Flugzeit, die sehr früh im Jahr ihren Höhepunkt erreicht. Nach Untersuchungen in Finnland beginnt die Flugaktivität von *T. laeve* bereits bei 13°C und erreicht ihren Höhepunkt bei 15°C, dem Schwellenwert für den Flugbeginn von *T. lineatum*. Die Flugperioden der beiden Arten überschneiden sich kaum. *T. laeve* scheint vor allem unter der Rinde von stehenden Bäumen, bzw. stehendem Totholz zu überwintern, was es der Art ermöglicht, auch bei noch geschlossener Schneedecke auszufliegen. Ab Frühjahr 2008 werden im Nationalpark Bayerischer Wald mittels Pheromonfalleneinsatz Verbreitung und Abundanzen von *T. laeve* genauer untersucht. Wünschenswert sind in Deutschland aber auch gezielte Untersuchungen in den Alpen und Mittelgebirgen.

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